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REVISION OF THE EASTERN PACIFIC SYNGNATHIDAE (PISCES:SYNGNATHIFORMES), INCLUDING BOTH RECENT AND FOSSIL FORMS

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Abstract: The marine and estuarine eastern Pacific Syngnathidae comprises 17 extant and 3 extinct species. Diagnostic characters for species and genera, including meristic and morphometric characters, and osteological features, are given. All species both living and fossil are diagnosed and described.

The recognized species and their ranges are: *Hippocampus ingens* Girard [=*H. hildebrandi*] (San Francisco Bay, California, south to Pucusana, Peru, including the Gulf of California); *Doryrhamphus melanopleura* (Bleeker) (Indo-Pacific; in the eastern Pacific from Bahía Magdalena, Baja California, south to Isla la Plata, Ecuador, including the Gulf of California, Galápagos Islands, and Clipperton Island); *Doryrhamphus paulus* n.sp. (Islas Revillagigedo, Mexico); *Leptonotus blainvilleanus* (Eydoux and Gervais) [=*S. acicularis*] (Hornitos, Chile, to Golfo Nuevo, Argentina); *Bryx arctus* (Jenkins and Evermann) (Tomales Bay, California, south to Mazatlán, Mexico, including the Gulf of California); *Bryx heraldi* n.sp. (Islas Juan Fernández and Isla San Félix, Chile); *Bryx coccineus* (Herald) (Bahía Banderas, Mexico, south to Punta Aguja, Peru, and the Galápagos Islands); *Bryx veleronis* Herald (Galápagos Islands; Islas Revillagigedo; Isla Murciélago and Isla del Caño, Costa Rica; and Islas San José and Canal de Afuera, Panama); *Bryx clarionensis* n.sp. (Isla Clarión, Mexico); *Syngnathus auliscus* (Swain) (Santa Barbara Channel, California, south to Paita, Peru, including the Gulf of California); *Syngnathus carinatus* (Gilbert) (confined to upper Gulf of California); *Syngnathus exilis* (Osburn and Nichols) (Half Moon Bay, California, to Bahía Magdalena, Baja California, and Isla Guadalupe, Mexico); *Syngnathus californiensis* Storer (Bodega Bay, California, south to Bahía Santa María, Baja California); *Syngnathus macrobrachium* n.sp. (Tumbes, Peru, south to Puerto Montt, Chile); *Syngnathus euchrous* n.sp. (Redondo Beach, California, to Punta Eugenia, Baja California); *Syngnathus leptorhynchus* Girard [=*S. griseolineatus*, *S. barbarae*] (southeastern Alaska south to Bahía Santa María, Baja California); *Syngnathus insulae* n.sp. (Isla Guadalupe, Mexico).

Studies of growth and variation show that *S. leptorhynchus* is highly variable with each population distinct. Marked seasonal variation, when combined with growth data, indicates that individuals probably live for one year or less.

The fossil pipefishes of Southern California are all only known from the Miocene. *Hipposyngnathus imporcitor* n.sp. from the upper Modelo Formation is most closely related to two species from the Oligocene of Europe. *Syngnathus emeritus* n.sp. is known only from the Puente Formation. *Syngnathus avus* Jordan and Gilbert is known from the lower Modelo Formation.

A comparison between inferred relationships of the various species and their geographical distribution suggests that the evolution of the eastern Pacific *Syngnathus* is a result of at least two separate invasions. *Doryrhamphus melanopleura* invaded the eastern Pacific by crossing the East Pacific Barrier and gave rise to *Doryrhamphus paulus*. *Leptonotus blainvilleanus* is related to other species of *Leptonotus* in New Zealand and southern Australia and was probably derived from an ancestor in these areas via waif dispersal.

The reduction and loss of elements of the branchial skeleton is useful in characterizing urophorine genera and may be of general use when relationships within the family Syngnathidae are studied in more detail.

Introduction

Pipefishes of the family Syngnathidae inhabit most temperate and tropical seas. In the eastern Pacific, pipefishes occur from southeastern Alaska to Tierra del Fuego. They are primarily marine or euryhaline, but some species are confined to fresh water.

Even though the family Syngnathidae contains the seahorses, of general interest to aquarists, the family has, in general, been poorly studied. There are a number of undescribed species and the intrafamilial relationships are poorly understood, due, in part, to the great variability in meristic and morphometric characters.

A revision of the Syngnathidae was published by Duncker (1915), but the American species were not included. Ginsburg (1937) and Herald (1940–1965) have been the major contributors to the taxonomy of the American syngnathids. To date, a definitive treatment of the eastern Pacific syngnathids has not appeared.

Detailed osteological work on adult syngnathids is limited to that of Jungersen (1910), Rauther (1925), and Banister (1967). Jungersen's study included the genera *Hippocampus, Syngnathus,* and *Nerophis,* two of which occur in the eastern Pacific. Rauther also studied the osteology of *Syngnathus,* as did Banister. The osteology of the other four genera of eastern Pacific syngnathids has not been treated. It is generally recognized that for the study of higher taxa, osteological characters are a good indicator of phylogeny because of their conservative nature.

The goal of this study has been to characterize the eastern Pacific genera and species of Syngnathidae, both fossil and recent, and to examine intraspecific variation. In addition, a preliminary examination of the osteology of a few of the syngnathid genera was made to help in understanding the relationships between at least a few of the genera, and as a test of the relationships proposed by Herald (1959) based on the method of brood-pouch closure.

Materials and Methods

Specimens that have contributed to the data are listed in the Material Examined section for each species. In those lists, the number of specimens is given, followed by the size range (SL in mm) enclosed in parentheses. If the size range was not determined or the specimens are damaged, the range of standard length is not given. Abbreviations for listed collections are: AMS, the Australian Museum, Sydney; BC, University of British Columbia: BMNH, British Museum (Natural History); BOC, Bingham Oceanographic Collection, Yale University; CAS, California Academy of Sciences; EMBCh, Estacíon de Biología Marina, Chile; GCRL, Gulf Coast Research Laboratory Museum; HSU, Humboldt State University; IMARPE, Instituto del Mar, Peru; LACM, Natural History Museum of Los Angeles County; MCZ, Museum of Comparative Zoology, Harvard University; MNHN, Muséum National d'Histoire Naturelle, Paris; MNMH P, Museo Nacional de Historia Natural, Santiago, Chile; SCCWRP, Southern California Coastal Water Research Project; SIO, Scripps Institution of Oceanography Marine Vertebrates Collection; SU, Stanford University (now housed at CAS); UCLA, Department of Zoology, University of California, Los Angeles; UMMZ, University of Michigan Museum of Zoology, USNM, National Museum of Natural History, Smithsonian Institution; UW, University of Washington.

Measurements were made with dial calipers to the nearest 0.1 mm for lengths less than 17 cm; an ocular micrometer was used for measurements less than 2 mm. Measurements greater than 17 cm were made to the nearest mm with a centimeter rule.

The principle characters used in identifying syngnathids are illustrated in Figures 1 and 2 (based on a generalized syngnathid). The terminology used for the various ridges on the body is that of Herald (1943).

The condition of the lateral trunk ridge (Fig. 2) is important in characterizing syngnathid genera. It is subcontinuous with the superior tail ridge in *Bryx* and *Syngnathus,* but continuous in *Leptonotus.* In *Hippocampus* and *Doryrhamphus* the lateral trunk ridge is continuous with the inferior tail ridge. Clausen (1956) has shown that these ridge patterns are not wholly consistent within species, however, they are of value when used with other characters.

Scutella (Fig. 1), small oval plates interpolated between the larger dermal plates, may be present or absent. Their size is important in species determinations and is therefore included in the species descriptions. Size is given as a comparison of an individual scutellum with an adjacent plate.

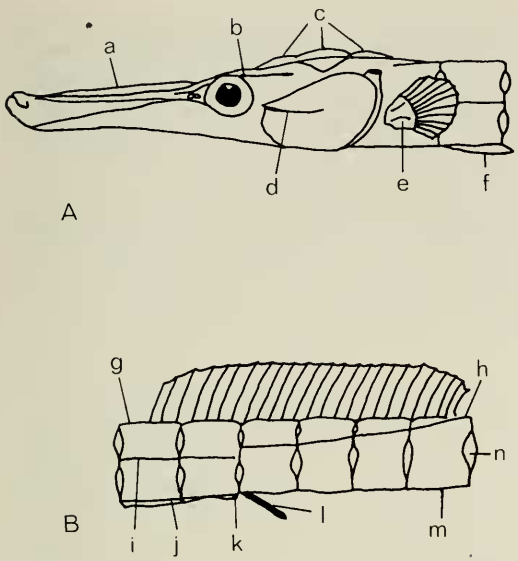

FIGURE 1. Characters used in syngnathid identification (modified after Herald 1943). (*A*) Characters in the region of the head: *a*. snout ridge; *b*. supraorbital ridge; *c*. supraoccipital, nuchal, and prenuchal ridges; *d*. opercular ridge; *e*. pectoral cover plate ridges; *f*. ventral trunk ridge. (*B*) Characters in the region of the dorsal fin: *g*. superior trunk ridge; *h*. superior tail ridge; *i*. lateral trunk ridge; *j*. inferior trunk ridge; *k*. anus; *l*. anal fin; *m*. inferior tail ridge; *n*. scutellum.

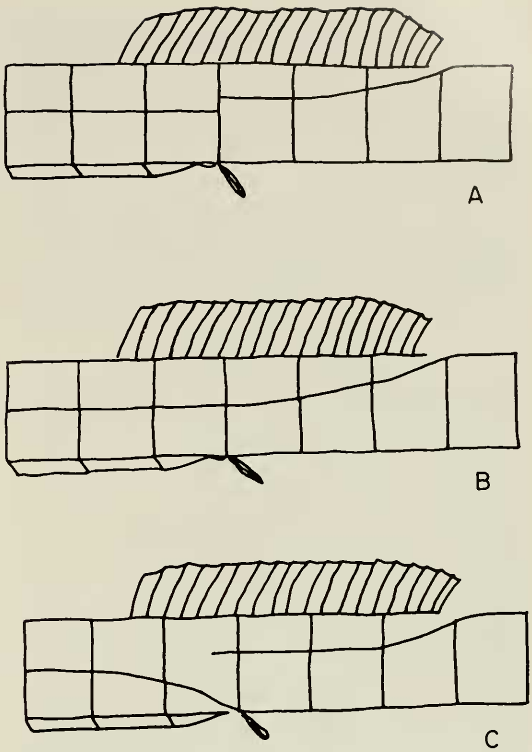

FIGURE 2. Configuration of ridges above the anus (modified after Herald 1943). (*A*) Lateral trunk ridge subcontinuous with superior tail ridge. (*B*) Lateral trunk ridge continuous with superior tail ridge. (*C*) Lateral trunk ridge continuous with inferior tail ridge.

A ring is defined as one unit in the series of dermal plates which form definite bands around the body.

Pouch protecting plates are not illustrated. They are merely ventral extensions of the inferior trunk or tail ridge which support the brood pouch and protect the eggs.

The pectoral cover plate is defined as the plate covering the base of the pectoral fin.

The methods of making counts and measurements are those of Hubbs and Lagler (1958), with the following exceptions:

Number of trunk and tail rings: The ring bearing the pectoral fins is counted as the first trunk ring; the ring bearing the anus is the last trunk ring. The ring bearing the anal fin is the first tail ring. If the anus and the anal fin are borne on the same ring, then that ring is the first tail ring and the preceeding ring is the last trunk ring.

Number of dorsal and anal fin rays: last two rays are counted as two.

Number of rings covered by dorsal fin: fractions of a ring estimated to the nearest tenth of a ring.

Number of lateral-line papillae: range of the number of lateral-line papillae per dermal plate.

For *Hippocampus* the standard length is the distance from the tip of the coronet, with the head held perpendicular to the trunk, to the tip of the tail, with the tail held straight (Ginsburg 1937).

In species diagnoses the modal range of a particular meristic character is given in parentheses after the range of that character.

Osteology was studied from trypsin-digested and alizarin-stained specimens (Taylor 1967) listed below. Osteological nomenclature follows Jungersen (1910) and Banister (1967). Bones were drawn with the aid of a camera lucida.

Diagnoses are based on adults unless otherwise noted.

Statistical procedures follow the text of Dixon and Massey (1957) except that the regression analyses are based on the Bartlett regression analysis as given by Hoese (1971). Unless otherwise specified, differences are considered significant at $P \leq .05$.

Cleared and Stained Material Examined.—*Heraldia nocturna*, SIO 75-54, 1, Sydney, Australia; *Maroubra perserrata*, SIO 75-53, 1, Sydney, Australia; *Choeroichthys brachysoma* SIO 73-196, 1, Timor Sea; *Doryrhamphus melanopleura*, SIO 65-343, 1, Gulf of California; *Dunckerocampus dactylophorus*, CAS uncat., 1, unknown; *Dentirostrum janssi*, CAS 14148, 3 paratypes, Thailand; *Syngnathoides biaculeatus*, SIO 61-693, 1, 10°N, 103°50'E; *Leptonotus blainvilleanus*, USNM 176569, 1, Isla Chiloé, Chile; *Leptonotus blainvilleanus*, USNM 176564, 1, Bahía Lin, Chile; *Parasyngnathus elucens*, CAS 13696, 1, Virgin Islands; *Ichthyocampus belcheri*, CAS uncat., 2, Philippine Is.; *Micrognathus brevirostris*, SIO 73-196, 4, Timor Sea; *Penetopteryx taeniocephalus*, SIO 66-587, 1, Great Tulear Reef; *Syngnathus carinatus*, S. Guevarra pers coll., 1, Gulf of California; *S. acus*, SIO 73-310, 1, Yugoslavia; *S. auliscus*, SIO 68-168, 1, Sonora, Mexico; *S. californiensis*, SIO H47-180, 1, Santa Cruz Island; *S. leptorhynchus*, E. B. Brothers pers. coll., 1, Mission Bay; *S. pelagicus*, SIO 65-358, 1, western Atlantic; *Bryx veleronis*, SIO 71-52, 1, Panama; *B. clarionensis*, SIO 74-116, 1, paratype, Clarion Is.; *B. dunckeri*, SIO 70-376, 1, Panama; *B. arctus*, SIO H52-218, 1, Baja California; *B. coccineus*, USNM 220972, 1, Galapagos Is.; *Cosmocampus brachycephalus*, CAS 24025, 2, Panama; *Corythoichthys flavofasciatus*, R. Nolan pers. coll., 1, Eniwetak; *Corythoichythys* sp., SIO 73-206, 1, Timor Sea, *Pseudophallus starksi*, USNM 208371, 2, Panama; *P. elcapitanensis*, USNM 208369, 1, Panama; *Hippocampus kuda*, SIO-60-250, 1, Hawaii; *H. ingens*, NMFS uncat., 1, eastern Pacific; *Phyllopteryx foliatus*, SIO 73-361, 1, Australia.

Systematics

Family **Syngnathidae** Bonaparte, 1838

Type-Genus: *Syngnathus* Linnaeus, 1758.

Diagnosis.—Syngnathiforms with body encased in armor formed of dermal plates arranged in rings; pelvic and spinous dorsal fins absent; dorsal and pectoral fins moderately developed to absent; caudal and anal fins weakly developed to absent (tail often prehensile when caudal fin absent); opercular slit reduced to a small opening at dorsoposterior margin of opercle, four complete gill arches bearing lobate gills; pseudobranchiae present; supracleithra and postcleithra absent; ribs absent; teeth lacking on jaws, but premaxillae and dentaries may bear odontoid processes (Dawson and Fritzsche 1975); pharyngobranchial tooth plates present or absent; upper part of cleithrum forms part of the external armor; posttemporals suturally united to neurocranium; 1–3 branchiostegals; no basisphenoid; no metapterygoid; eggs incubated by males in a special area under the trunk or tail, which may or may not be developed into a pouch; no pyloric sphincter; no distinct stomach; right kidney only present, aglomerular; predorsals reduced to 2–3 nuchal plates.

The family is usually divided into two groups: Gastrophori—those which develop the brood pouch under the abdomen; Urophori—those with the brood pouch under the tail.

Key to Genera of Eastern Pacific Syngnathidae

1a. Caudal fin absent; tail prehensile; head at right angle to main body axis .... *Hippocampus* Rafinesque
1b. Caudal fin present; tail never prehensile; head in line with main body axis 2
2a. Brood pouch under abdomen 3
2b. Brood pouch under tail 4
3a Trunk rings more numerous than tail rings .... *Doryrhamphus* Kaup
3b. Trunk rings fewer than tail rings .... *Oostethus* Hubbs
4a. Lateral trunk ridge continuous with superior tail ridge; brood pouch without protecting plates; mature females with deep, compressed trunk .... *Leptonotus* Kaup
4b. Lateral trunk ridge subcontinuous with superior tail ridge; brood pouch with protecting plates; mature females with subcylindrical trunk 5
5a. Dorsal rays 23 or fewer; snout short, contained 2.3–4.0 times in head; anal fin present or absent; small, never longer than 124 mm SL .... *Bryx* Herald
5b. Dorsal rays 26 or more; snout longer, contained 1.6–2.8 times in head; anal fin present; larger, most species reach 200 mm or more SL .... *Syngnathus* Linnaeus

Records of Doubtful Validity

Regan (1908) included *Oostethus brachyurus* (Bleeker) and *Syngnathus spicifer* Rüppell in his list of the fishes occurring at Tehuantepec, Mexico. Herald (1940) repeated these records but doubted their validity. Herald (1943) indicated that there was considerable doubt that these two species were collected at Tehuantepec, because he had been able to confirm that Regan's specimens had come from an animal dealer. Duncker (1915) had also realized that the specimens had come from an animal dealer, but the records have persisted. The animal dealer had received specimens from both Mexico and the Philippines. *O. brachyurus* and *S. spicifer* occur in the Philippines, and it seems most probable that the specimens were collected there.

There is, however, a valid record of *Oostethus* from the eastern Pacific. McCosker and Dawson (1975) reported a single individual of the euryhaline Atlantic *Oostethus lineatus* collected on the Pacific side of Panama in 1971 and concluded that the specimen represents a transit of the Panama Canal.

Dermatostethus punctipinnis Gill (1863) was described from four specimens collected at San Diego. Presently there are three type-specimens at the USNM (lectotype, here designated as USNM 8128; paralectotypes here designated as USNM 214484). Much confusion has been generated by these specimens. The types are quite large (302–344 mm SL), have a very flexible "neck," and dark spotting on the dorsal fin. Herald (1940, 1941) referred *D. punctipinnis* to the synonymy of *Syngnathus californiensis* because the latter is a large species with counts like that of the type material of *D. punctipinnis*. Miller and Lea (1972:212) suggested that *D. punctipinnis* might be a valid species, but did not include it in their key to California species. I have examined the types of *D. punctipinnis* and have compared them to specimens of *S. acus* from Europe and have been unable to find significant differences. I therefore relegate *D. punctipinnis* to the synonymy of *S. acus*.

Syngnathus acus has been recorded from the Indo-Pacific (Weber and De Beaufort 1922), and my examination of a specimen from that region (Pakoi, China) suggests the existence of a distinct *acus*-like species. But the putative California material is typical of *acus* and could not represent trans-Pacific migration.

Duméril (1870) described *Syngnathus bairdianus* from a locality given as "Côte du Mexique, voisine de la Californie." The locality as listed in the catalog of the MNHN is "Mexique près la Californie, Lucas 1867." I examined the two types (lectotype, here designated as MNHN 6112; paralectotype, here designated as MNHN 2756) and found them to be indistinguishable from *S. pelagicus* Linnaeus. I therefore relegate *S. bairdianus* to the synonymy of *S. pelagicus*. *S. pelagicus* inhabits the Sargasso Sea and apparently can be transported over long distances. It has been recorded from Tierra del Fuego (Fowler 1944) and from New Zealand (Weber and De Beaufort 1922). *Histrio histro*, another inhabitant of the Sargasso Sea, is widely distributed and has been recorded from the Galápagos Islands (Schultz 1957). It is therefore remotely possible that *S. pelagicus* could have been collected near the coast of Mexico.

None of the above species will be treated further because of their doubtful standing as members of the eastern Pacific fauna.

Hippocampus Rafinesque

Hippocampus RAFINESQUE, 1810:18 (type-species by monotypy, *H. heptagonus* Rafinesque [=*Syngnathus hippocampus* Linnaeus]); DUNCKER 1912:237 (diagnosis); 1915:115 (diagnosis); GINSBURG 1937:525 (diagnosis; discussion).

Farlapiscus WHITLEY, 1931:313 (type-species by original designation, *Hippocampus breviceps* Peters).

Hippohystrix WHITLEY, 1940:44 (type-species by original designation, *Hippocampus spinosissimus* Weber).

DIAGNOSIS.—Urophori characterized by a prehensile tail; absence of caudal fin, scutella, brood pouch protecting plates, and basibranchials; head at right angle to trunk; brood pouch sealed along midline except for small anterior opening; occiput raised to form coronet; dorsal fin base raised.

DISTRIBUTION.—Marine; world-wide in tropical and subtropical seas.

Hippocampus ingens Girard

(Figures 3 & 7C)

Hippocampus ingens GIRARD, 1859:342 (original description; San Diego, California) (lectotype here designated as USNM 982); JORDAN AND GILBERT 1880:23 (San Diego); 1881:453 (San Diego); JORDAN AND JOUY 1881:1 (California); JORDAN AND GILBERT 1882:69 (San Diego); 1883:386 (description; range); EVERMANN AND JENKINS 1891:127, 135 (Guaymas, Mexico); GILBERT 1891:450 (ALBATROSS sta. 2795); EIGENMANN AND EIGENMANN 1892:144 (San Diego); VAILLANT 1894: 70 (Gulf of California); JORDAN 1895:417 (description; Mazatlán, Mexico); JORDAN AND EVERMANN 1896:776 (synonymy; description); GILBERT AND STARKS 1904:57 (Panama Bay); GILL 1905:807 (range); STARKS AND MORRIS 1907:186 (range); OSBURN AND NICHOLS 1916:155 (Concepción Bay); NICHOLS AND MURPHY 1922:506 (Peru); MEEK AND HILDEBRAND 1923:256 (description; synonymy); BREDER 1928:23 (Cape San Lucas, Concepción Bay); ULREY AND GREELEY 1928:41 (synonymy; range); ULREY 1929:6 (Lower California, Gulf of California); 1932:77 (Baja California); GINSBURG 1937:534 (range; synonymy; description); ATZ 1937:62 (size); FOWLER 1944:496 (range); KOEPCKE 1962:200 (references; range); CLEMENS AND NOWELL 1963:262 (off Mexico; in stomachs of fish); HUBBS AND HINTON 1963:12 (California record; range); CHIRICHIGNO-F. 1963:8, 34 (Peru; range); CASTRO-AGUIRRE ET AL. 1970:132 (common in Gulf of California); MILLER AND

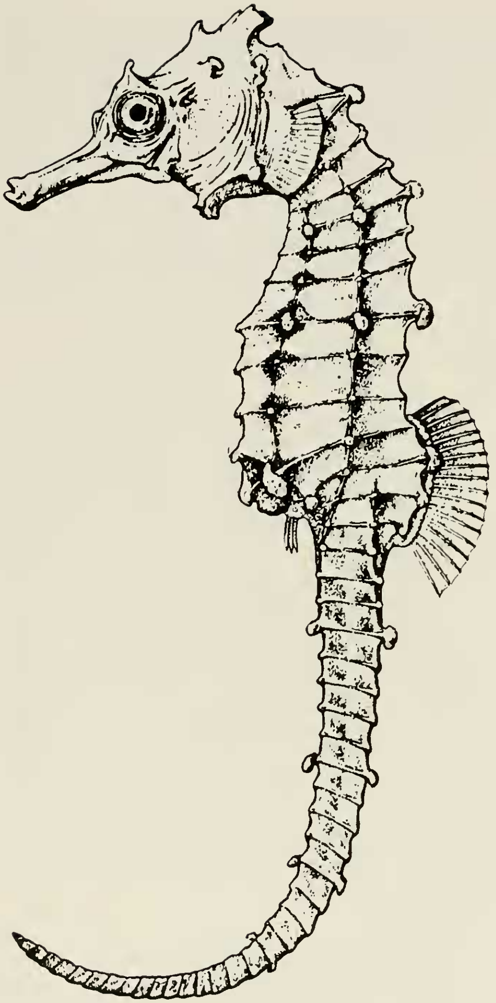

FIGURE 3. *Hippocampus ingens*, MCZ 35292, collected in 1860 at San Francisco, California, by Alexander Agassiz (not examined).

LEA 1972:89 (description; range); CHIRICHIGNO-F. 1974: 86, 337 (Peru; in key; range).

Hippocampus gracilis GILL, 1863:282 (original description; Cape San Lucas, Baja California).

Hippocampus ecuadorensis FOWLER, 1921:446 (original description; Bahía, Ecuador).

Hippocampus hildebrandi GINSBURG, 1933:562 (original description; Chame Point, Panama); holotype USNM 82063); 1937:579 (description; range).

DIAGNOSIS.—A *Hippocampus* with 17–22 (19) dorsal rays; 15–17 pectoral rays; 4–5 anal rays; 11–12 (11) trunk rings; 37–41 (39) tail rings; dorsal fin on 1.2–2 + 1.5–4 rings; total rings covered by dorsal fin 3–4; brood pouch on 5–8 rings; head 4.2–5.8 in SL; dorsal fin base 1.8–2.9 in head; snout 1.8–2.5 in head; maximum size examined 247 mm SL; smallest mature male 54 mm, said to attain 12″ (297 mm) (Miller and Lea 1972), which is approximately the size of my largest specimen if the head is included in the measurement.

DESCRIPTION.—Body ridges typically well developed with a blunt recurved tubercle at center of each plate. First, fourth, seventh, and tenth trunk rings usually with larger and better developed tubercles. Sixth, tenth, fourteenth, and eighteenth tail rings may have strongly developed tubercles, but are usually more obsolescent than trunk tubercles. Coronet with five radially arranged tubercles. Males with the more weakly developed tubercles. Tubercles in both sexes generally become obsolete with growth. Strong nuchal ridge, without spines. Opercle with faint radiating striae. No prominent snout ridge. Internasal spine blunt. Prominent broad-based supraopercular spine directed laterally. Lateral trunk ridge and superior tail ridges overlap for one ring. Trunk rings octangular under dorsal fin, heptangular anteriorly. Trunk moderately compressed. First tail ring heptangular, remainder quadrangular. Superior trunk and tail ridges overlap for two to three rings. Dermal flaps, when present, on enlarged tubercles and head ridges, consisting of a stout base with numerous filamentous outgrowths.

Coloration in life. Red, yellow, or green. One specimen captured at La Paz, Baja California, had undersides and tips of tubercles yellowish, most of body mottled with dark brown to black, and covered with many small dark spots as well as smaller white ones. The white spots tend to coalesce into longitudinal streaks; yellowish coloration more pronounced on underside of tail. White bands around body every six or seven rings. Dorsal fin with distinct dark submarginal band. Pectoral fins hyaline.

Coloration in alcohol. Enlarged tubercles usually whitish, often with white ring around body at that point. Ground color dark brown with small white papillae often forming streaks and reticulations, and radiating lines around orbit. Ventral surface of tail without white markings. Dorsal fin with a dark band near margin. Median abdominal ridge often dark brown in males. However, color variable; some specimens may be uniform light tan.

HABITAT.—Collections of *H. ingens* are uncommon. Some have been made in shallow water, but most specimens have been captured at depth with dredges or trawls, or at the surface in the open ocean. Dredge and trawl collections have usually been made at depths of 10 m or more. Juveniles (ca. 40 mm) and larger individuals (115 mm) are not uncommonly taken at the surface. Alverson (1963) studied the food items in stomachs of eastern Pacific yellowfin tuna, *Thunnus albacares*, and found *H. ingens* in 18 stomachs out of the 2846 he examined. Judging from the small displacement volumes of these fish, they were all juveniles. One 34-mm individual (SIO 71-186) was taken from the gut of a bluefin tuna, *Thunnus thynnus*. The habitat is not yet precisely known. *H. ingens* appears to spend much of its life in the open sea.

COMPARISONS.—Ginsburg (1933) described *H. hildebrandi* from Chame Point, Panama, as differing from *H. ingens* in having lower, broader tubercles. My examination of 38 specimens from the eastern Pacific has shown that all specimens are referrable to *H. ingens*. I have examined the types of *H. ingens* and *H. hildebrandi* and conclude that the types of *H. hildebrandi* are juveniles of *H. ingens*.

Since *H. ingens* is the only species of seahorse in the eastern Pacific, it is easily identifiable. The closest relative of *H. ingens* is possibly *H. reidi* Ginsburg from the western Atlantic, from which it differs in number of dorsal rays (17–22 vs 15–19) and in number of tail rings (36–41 vs 34–37). The relationship of *H. ingens* to seahorses of the Indo-Pacific is impossible to determine because knowledge of the genus *Hippocampus* is very incomplete.

RANGE.—San Francisco Bay, California, south to Pucusana, Peru, including the Gulf of California. Infrequently taken north of central Baja California. During periods of unusually warm water, *H. ingens* may enter California waters.

MATERIAL EXAMINED.—**California:** San Diego, USNM 982, 1(167), lectotype; USNM 214485, 2(125–146), paralectotypes; Point Loma, SIO 63-1085, 1(195).

Baja California: Laguna Guerrero Negro, SIO 61-10, 3(155–185). Bahía Sebastián Vizcaíno, SIO 63-1046, 1(29). Bahía Magdalena, SIO 62-713, 1(108); SIO 64-73, 1(27); SIO 60-305, 1(55). Punta Hughes, SIO 64-45, 1(109).

Gulf of California: La Paz, SIO 74-81, 1(200). Punta Mangles, SIO 65-335, 1(122). Isla Santa Inéz, SIO 65-306, 1(99). San Felipe, SIO 67-1, 1(168).

Mazatlán South: Boca Teacapán, SIO 60-90, 1(118). Nayarit, SIO 60-89, 1(92). Bahía de Banderas, SIO 62-29, 1(148). Acapulco, UCLA W52-119, 1(70). Golfo de Tehuantepec, SIO 73-258, 5(116–136); SIO 68-16, 1(47); SIO 63-1031, 1(115); SIO 72-123, 1(80). Guatemala, SIO 63-623, 1(70); UCLA W56-273, 1(120). Costa Rica, UCLA W54-139, 1(114). Panama, SIO 71-260, 1(115); SIO 71-186, 1(36); USNM 82063, 1(66), holotype of *H. hildebrandi*; USNM 82037, 1(44), paratype of *H. hildebrandi*; USNM 82039, 1(47), paratype of *H. hildebrandi*.

Galápagos Islands: BC 56-440, 2(238–247); SIO 54-174, 1(128). Isla Santa Cruz, SIO H51-388, 1(89).

Doryrhamphus Kaup

Doryrhamphus KAUP, 1853:233 (nomen nudum); 1856:54 (type-species by monotypy, *D. excisus* Kaup; Red Sea); DUMÉRIL 1870:585 (description); JORDAN AND EVERMANN 1896:773 (in part; description); DUNCKER 1912:231 (description; synonymy); 1915:244 (description; synonymy); JORDAN, EVERMANN, AND CLARK 1930:243 (synonymy); HERALD 1953:244 (description; synonymy).

Pristidoryrhamphus FOWLER, 1944:158 (type-species by original designation, *P. jacksoni* Fowler =*Doryrhamphus negrosensis* Herre).

DIAGNOSIS.—Gastrophori with lateral trunk ridge continuous with inferior tail ridge; inferior trunk and tail ridges discontinuous; superior trunk and tail ridges discontinuous; trunk rings more numerous than tail rings; snout ridge strongly serrate, markedly so in mature males; each dermal plate armed with strong retrorse spine; no pouch-protecting plates; caudal fin large and brightly colored; branchial skeleton with all elements present; scutella present; two nuchal plates; three infraorbitals; strongly developed opercular ridge; 14–19 trunk rings; 10–17 tail rings; 21–29 dorsal rays; 4 anal rays; 10 caudal rays.

RANGE.—Four or five species ranging throughout the tropical Indo-Pacific among coral and rocky reefs.

DISCUSSION.—Kaup first published the name *Doryrhamphus* in 1853, but his reference to *D. excisus* Hemprich and Ehrenberg cannot be taken to be an indication as defined by the *International Code of Zoological Nomenclature* Art. 16a(v). The species *D. excisus* was an unpublished manuscript name in 1853. The requirements of the Code were not fulfilled until Kaup (1856) published descriptions of *Doryrhamphus* and *D. excisus*.

Key to Eastern Pacific Species of *Doryrhamphus*

1a. Trunk rings 16–18 (usually 17) tail rings 14–17 (usually 15); head 4.0–4.4 in SL .... *melanopleura* (Bleeker)
Tropical Indo-Pacific

1b. Trunk rings 16–17 (usually 16); tail rings

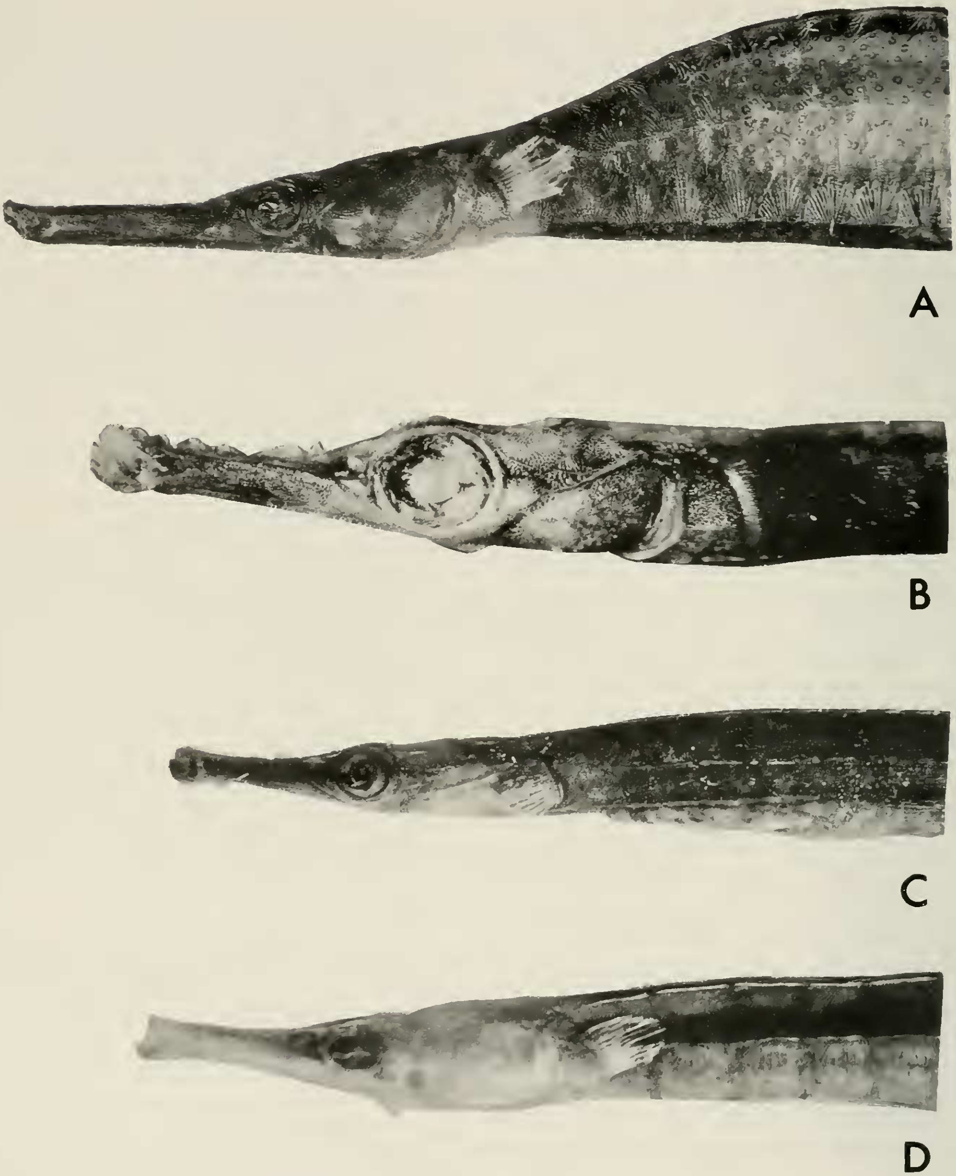

FIGURE 4. Anterior part of body of four species of eastern Pacific Syngnathidae. (*A*) *Leptonotus blainvilleanus*, a 168-mm-SL female, SIO 72-168. (*B*) *Doryrhamphus paulus*, holotype, SIO 72-67. (*C*) *Doryrhamphus melanopleura*, a 52-mm-SL male, SIO 65-343. (*D*) *Syngnathus auliscus*, a 110-mm-SL female, SIO 65-181.

13–15 (usually 14); head 3.4–4.0 in SL .... *paulus* n.sp.
Islas Revillagigedo, Mexico

Doryrhamphus melanopleura (Bleeker)

(Figure 4*C*)

Syngnathus melanopleura BLEEKER, 1858:464 (original description; "Kokos-eilanden").

Doryrhamphus californiensis GILL, 1863:284 (original description; Cabo San Lucas; holotype SU 19255); JORDAN AND EVERMANN 1896:773 (description; range); DUNCKER 1915:62 (as "species dubia"); ULREY 1929: 6 (Cape San Lucas); JORDAN, EVERMANN, AND CLARK 1930:243 (range); ULREY 1932:77 (Cabo San Lucas); NICHOLS AND MURPHY 1944:239 (Panama); FOWLER 1944:496 (range).

Doryichthys californiensis: GÜNTHER 1870:186 (new combination; description; range).

Microphis extensus SNYDER 1911:525 (original description; Naha, Okinawa; holotype USNM 98266).
Doryrhamphus melanopleura: HERALD 1940:59 (in key; synonymy; range); 1953:246 (description; subspecies; range).

DIAGNOSIS.—A *Doryrhamphus* with 22–27 (24–25) dorsal rays; 19–23 pectoral rays; 16–18 (17) trunk rings; 14–17 (15) tail rings; dorsal covering 3–5 + 2–4 rings; total rings covered by dorsal fin 6–7.5; brood pouch covering 17–19 rings; head 4.0–4.4 in SL; dorsal fin base 1.6–1.9 in head; snout 2.0–2.5 in head; maximum known size 69 mm SL; smallest mature male 31 mm SL.

DESCRIPTION.—A sharply ridged and strongly spined fish. Head with prominent prenuchal, nuchal, and occipital crests. Snout ridge strongly serrated, markedly so in mature males. Pectoral cover plate with well-developed superior and inferior ridges. Strong spination on maxillae and along dorsal edge of infraorbitals. Ventral edge of quadrate occasionally with strong serrations. Each ring bears a single posteriorly directed spine on each ridge, becoming obsolete along ventral ridges. Scutella large. No dermal flaps.

Brood pouch abdominal, without protecting plates. Eggs about 0.5 mm in greatest diameter, arranged in three layers, four across. Males with eggs and young collected from March through August.

Fins all large and well developed. Caudal a little longer than snout. Dorsal base about equal to snout and orbit combined. Anal conspicuous, its length about half orbital diameter. Pectoral fins broad based.

Coloration in life. Essentially the same as coloration in alcohol except that caudal has a white border, two yellowish spots near base, and an oval orange area in middle part of fin.

Coloration in alcohol. Uniform dusky with darker streak from tip of snout to pectoral base. Fins colorless except for caudal, which is distinctively marked with two light basal spots and one larger median spot. Individual fin rays often lined with melanophores on each side. Young less than 20 mm SL have a banded color pattern with eight brown bands on a lighter background.

HABITAT.—In crevices in rocks, under overhangs, and among coral heads.

RANGE.—In eastern Pacific from Bahía Magdalena, Baja California, south to Isla la Plata, Ecuador (UMML), and at the Galápagos Islands and Clipperton Island. In the Gulf of California north to Isla Ángel de la Guarda (UCLA W60-6, not examined) in the west to Punta Guillermo, Sonora (UCLA W51-11 not examined), in the east. Widely distributed throughout Indo-Pacific.

COMPARISONS.—*D. melanopleura* is an interesting and complex species. It has been divided into several subspecies (Herald 1953) that are probably not valid. A detailed study of the populations is needed before much can be said about possible relationships. It is related to *D. paulus* from which it can be distinguished by the characters given in the description of that species.

MATERIAL EXAMINED.—**Mexico:** Bahía Magdalena, SIO 64-54, 3(55–62). Cabo San Lucas, SIO 61-227, 10(18–56). Los Frailes, SIO 61-249, 14(32–64). Bahía de los Muertos, SIO 74-90, 3(32–46). Isla San José, SIO 65-265, 5(48–55). Isla Santa Cruz, SIO 65-343, 6(19–61). Isla Carmen, SIO 65-302, 15(45–62). Isla San Ignacio de Farallón, SIO 59-228, 3(40–42). Lobos Rock, SIO 61-280, 20(16–53). Bahía de Banderas, SIO 62-29, 2(29–45).

Costa Rica: Isla del Caño, LACM 32548, 36(33–55).

Panama: Taboguilla Island, SIO 67-34, 21(16–48).

Galápagos Islands: Plaza Island, SIO 64-1015, 3(53–63); BC 54-392, 1(64).

Comparative material from Indo-West Pacific: Hawaii, CAS 20402, 1(54). Eniwetak, R. S. Nolan personal collection, 3(39–45). Guam, CAS 15835, 2(44–44). Australia, AMS IA-2713, 1(38); AMS I10740, 2(31–39). Japan, CAS 14512, 2(68–69).

Doryrhamphus paulus n.sp.

(Figure 4*B*)

Doryrhamphus melanopleura pleurotaenia: (in part) HERALD 1953:248 (size; meristic data).
Doryrhamphus melanopleura: Ricker 1959:2 (Socorro Island).

DIAGNOSIS.—A dwarf species of *Doryrhamphus* with 23–26 dorsal rays; 20–21 pectoral rays; 16–17 (16) trunk rings; 13–15 (14) tail rings; 29–31 (30) total rings; dorsal on 3–4.2 + 2.5–4 rings; total rings covered by dorsal fin 6.5–7.5; brood pouch on 14–17 rings; head 3.4–4.0 in SL; dorsal fin base 1.7–2.2 in head; snout 2.1–2.7 in head; smallest mature male 24.5 mm SL; maximum known size 38.9 mm SL.

DESCRIPTION.—Strongly ridged and spined. Occipital, nuchal, and prenuchal ridges low but sharply defined. Snout ridge serrate in males, with 4–5 spines on anterior tip and three or so larger isolated spines further posterior; females and juveniles with or without obvious snout-ridge serrations. Pectoral cover plate with superior and inferior ridges. Each body plate with a sharp retrorse spine. No dermal flaps.

Only one brooding male known, collected in March.

Fins well developed. Caudal shorter than snout. Dorsal fin base equal to combined snout and orbit. Pectoral fins broad based but short, only extending posteriorly to junction of first and second trunk rings.

Coloration. Essentially same as that given for eastern Pacific populations of *D. melanopleura*.

HABITAT AND RANGE.—Three to 17 m, among rock reefs in Islas Revillagigedo, Baja California.

COMPARISONS.—*D. paulus* is most closely related to, and was probably derived from, *D. melanopleura*, which is widespread in the Indo-Pacific but is not represented at the Islas Revillagigedo. Although *D. melanopleura* ranges throughout the Indo-Pacific and is quite variable, the number of trunk rings is fairly stable at 18. Some populations have modal counts of 17 or 19 rings; however, 16 trunk rings have never been found in *D. melanopleura*.

Doryrhamphus paulus can be distinguished from *D. melanopleura* by the characters given in the key.

D. excisus from the Red Sea also has 16 trunk rings, but differs from *D. paulus* in having 10–11 tail rings rather than 13–15, and 18–20 dorsal rays rather than 23–26.

ETYMOLOGY.—From the Latin *paulus*, little.

MATERIAL EXAMINED.—**Holotype:** SIO 72-67, a 32.7-mm-SL mature male collected at a depth of 6–12 m with Chemfish, ca. 100 m SE of "Humpback Cove," Isla Socorro, Islas Revillagigedo, Mexico, 19 Feb. 1972, by D. Diener and party.

Paratypes. Mexico. Islas Revillagigedo: SU 67255, 24.5 mm SL, mature male, 8 m, rotenone, "Grayson's Cove," Isla Socorro, 11 Mar. 1940, by Vernon Brock. SU 36442, 1(31), same data as SU 67255. CAS 13699, 9(20–34) and LACM 31781-2, 3(22–32), "Grayson's Cove," ca. 200 m N of "Old Man of the Rocks," Isla Socorro, R/V SEARCHER sta. 52, 8–12 m, rotenone, 14 Feb. 1971. LACM 317821-12, 5(26–32), S of Cape Henslow, Isla Socorro, R/V SEARCHER sta. 53, 13–17 m, rotenone, 15 Feb. 1971. GCRL 15753, 1(27), Braithwaite Bay, Isla Socorro, 3 m, rotenone, 13 Feb. 1956, by George Lindsay. SIO 72-67, 6(16–26), collected with holotype. SIO 74-155, 2(29–39), Sulfur Bay, Isla Clarión, 10–17 m, rotenone, 11 Dec. 1974, by Robert Kiwala.

Leptonotus Kaup

Leptonotus KAUP, 1853:232 (type-species by monotypy, *Syngnathus blainvilleanus* Eydoux and Gervais, 1837); 1856:46; DUNCKER 1912:235; 1915:88.

Acmonotus PHILLIPI, 1896:382 (type-species by original designation, *Acmonotus chilensis* Philippi [=*S. blainvilleanus* Eydoux and Gervais]).

Novacampus WHITLEY, 1955:110 [type-species by original designation, *Syngnathus norae* (Waite)].

DIAGNOSIS.—Urophori without pouch-protecting plates; trunk compressed and much expanded in females; lateral ridge system of the ascending pattern (Fig. 2*B*); all elements of branchial skeleton present, none reduced; dorsal fin usually located on two or more trunk rings; 10 caudal rays; opercular ridge weak or absent; most body ridges smooth and reduced; two branchiostegals.

DISTRIBUTION.—Approximately five species known only from south temperate seas; South America, South Australia, Tasmania, and New Zealand.

Leptonotus blainvilleanus (Eydoux and Gervais)

(Figure 4*A*)

Syngnathus blainvilleanus EYDOUX AND GERVAIS, 1837:79 (original description; "Mare Indicum"; holotype MNHN 6050); GUICHENOT 1848:348 (description).

Syngnathus acicularis JENYNS, 1842:147 (original description; Valaparaíso, Chile; holotype BMNH 1917.7.14.28).

Leptonotus Blainvillei: KAUP 1853:232 (range); 1856:16 (description; range).

Syngnathus blainvillianus: GÜNTHER 1870:162 (description; range); STEINDACHNER 1898:331 (Chile); THOMPSON 1816:423 (Patagonia).

Hemithylacus Petersi DUMÉRIL, 1870:600 (original description; Puerto Montt, Chile).

Acmonotus chilensis PHILIPPI, 1896:382 (original description; Pelluhue, Chile).

Leptonotus blainvillianus: ABBOTT 1899:338 (references; range); DUNCKER 1915:88 (synonymy; description; range); NORMAN 1937:40 (Patagonia); HERALD 1940:59 (synonymy; range); 1942:132 (diagnosed in key); FOWLER 1944:496 (range); MANN 1954:189 (description; range); DE BUEN 1963:89 (synonymy; description); KOEPCKE 1962:200 (range); CHIRICHIGNO-F. 1974:339 (in keys; range).

Syngnathus blainvillei: DELFIN 1901:43.

Siphostoma blainvilliana: EVERMANN AND RADCLIFFE 1917:53.

Leptonotus blaenvillianus: SICCARDI 1954:211–242 (brood pouch; variation).

Leptonotus blainvilleanus: DUMÉRIL 1870(2):581 (description; habitat); VAILLANT 1888:16 (Orange Bay, Patagonia; coloration); HERALD 1965:364 (common name).

DIAGNOSIS.—A *Leptonotus* with 34–41 (35–37) dorsal rays; 12–14 pectoral rays; 2–3 anal rays; 18–20 (19) trunk rings; 48–52 (50) tail rings; 67–70 total rings; dorsal on 0.5–2 + 7–8.2 rings; total rings covered by dorsal fin 7.3–10; brood pouch on 10–14 rings; head 7.0–9.0 in SL; dorsal fin base 1.0–1.6 in head; snout 1.8–2.2 in head; maximum known size 217 mm SL (Duncker 1915); smallest mature male 108 mm SL. See Table 1 for meristic variation.

DESCRIPTION.—Ridges on head and body mostly obsolete. Nuchal and prenuchal ridges low and smooth. Opercles strongly convex; opercular ridge reduced to basal one-fourth of

TABLE 1. MERISTIC VARIATION IN *Leptonotus blainvilleanus*.

	Trunk rings			Tail rings					Dorsal rays							
Locality	18	19	20	48	49	50	51	52	34	35	36	37	38	39	40	41
Chile:																
Antofagasta	1	12	1	1	3	6	4	—	2	6	1	4	1	—	—	—
Valparaíso	—	—	2	—	—	1†	1	—	—	—	—	1†	—	—	—	—
Concepción	—	1	—	—	—	—	1	—	—	—	—	1	—	—	—	—
Coquimbo	—	2	—	—	—	1	1	—	1	—	—	—	—	—	—	—
Puerto Montt	1	4	2	1	2	4	—	—	—	—	1	3	3	—	—	—
Isla Chiloé	—	9	3	4	4	4	—	—	—	2	3	4	2	—	—	—
Totals	2	28	8	6	9	16	7	—	3	8	5	13	6	—	—	—
		$\bar{x}$ = 19.1				$\bar{x}$ = 49.6						$\bar{x}$ = 36.3				
Argentina*:																
Golfo Nuevo																
(females)	27	4	—	—	4	16	10	1	—	1	1	8	14	5	1	1
(males)	3	34	3	5	12	20	—	2	—	—	7	7	13	8	1	1
Totals	30	38	3	5	16	36	10	3	—	1	8	15	27	13	2	2
		$\bar{x}$ = 18.6				$\bar{x}$ = 49.8						$\bar{x}$ = 37.8				
"Mare Indicum"**	—	1**	—	—	—	—	—	—	1**	—	—	—	—	—	—	—

† Holotype of *S. acicularis*.
* Data from Siccardi 1954.
** Holotype of *L. blainvilleanus*.

opercle, striations faint. Snout ridge smooth, low, and reaches posteriorly to interorbit. Supraorbital ridges smooth, one-half orbit diameter in length. Pectoral cover plate without ridges. Trunk of mature females compressed and expanded dorsoventrally, with sharp dorsal and ventral borders. Scutella small, indistinct. Plates with reduced ridgelets. Entire body very fleshy over plates. Lateral line papillae 2–4 per plate. No dermal flaps.

Brood pouch without lateral protecting plates. Males brooding eggs have been collected in January and March.

Dorsal fin high, its height equal to width of two trunk rings.

Coloration in alcohol. Juveniles with alternating pattern of dark and light bands along length of body. Darker bands about four rings in width, light bands only one-half a ring in width. Caudal dark brown with a light border. Snout and interorbit darker than remainder of head. Fins colorless.

Adult females sometimes entirely light tan with dark brown venter and dorsum on trunk, and with posterior half of tail dark brown. Usually the head is a dark olive-brown and the trunk is dark brown with small, dark-bordered ocelli. Dorsal fin may have a few melanophores along the ray margins. Adult males yellowish brown with dark brown area surrounding the nares; ocelli may develop on the first few tail rings.

HABITAT.—Kelp beds along the open coast; occasionally into brackish water (Fischer 1963).

REMARKS.—Meristic data from the Golfo Nuevo, Argentina, population of *L. blainvilleanus* (Table 1) (from Siccardi 1954) show a difference in mean number of trunk rings between males and females from Golfo Nuevo ($P \ll .005$).

The lower number of trunk rings in the Golfo Nuevo females contributes to the significant difference between the Chilean and Argentinean populations ($P \ll .005$). However, the dorsal ray count also differs significantly between these two regions.

Siccardi (1954) studied a large number of specimens of *L. blainvilleanus* from both coasts of southern South America and was able to provide some data on morphometric variation. She found that the depth of the trunk in males remains fairly constant during growth, from 112–140 mm, so that the standard length/trunk depth ratio was 22.4 in 112-mm fish and 26.7 in 140-mm fish. Also, the maximum depth of the trunk in females was attained by a standard length of 140–150 mm. This was correlated with reaching sexual maturity. The trunk in males became relatively shorter and the tail longer with growth, whereas relative lengths of the trunk and tail in females remained constant with growth.

COMPARISONS.—Because the genus *Leptonotus* has not received systematic treatment, it can only be said that *L. blainvilleanus* seems to be most closely related to the southern Australian species *L. semistriatus*. *L. blainvilleanus* can be distinguished from *L. semistriatus* by the snout length (1.8–2.2 in head rather than 1.6–1.7) and by the dorsal fin placement (on 0.5–2 + 7–8.2 rings rather than 3–4 + 7).

Leptonotus blainvilleanus has long been considered to be a member of the New Zealand fauna (Waite 1909). However, a comparison of the holotype of *L. blainvilleanus* with specimens of *Leptonotus* from New Zealand reveals that *L. blainvilleanus* and examined New Zealand species of *Leptonotus* are distinct. The New Zealand specimens of *Leptonotus* are referable to *L. elevatus* (Hutton) and *L. norae* (Waite).

Mr. A. Wheeler (BMNH) examined the holotype of *Syngnathus acicularis* Jenyns at my request. His counts and description of lateral ridge pattern confirm the fact that the holotype of *S. acicularis* is conspecific with *L. blainvilleanus*.

RANGE.—Hornitos, Chile, to Golfo Nuevo, Argentina.

MATERIAL EXAMINED.—"Mare Indicum," MNHN 6050, holotype.

Chile: Hornitos, SIO 72-168, 1(168). Antofagasta, EBMCh 1520-28, 9(86-207); GCRL 12466, 4(117–215). Coquimbo, MNMHP 5302, 1(169); MNMHP 5305, 1(246); Valparaíso, EBMCh 222, 1(190). Concepción, MNMHP 5574, 1(126). Bahía Lin, USNM 176564, 4(75–121). Puerto Montt, USNM 205179, 3(104–129). Isla de Chiloé, USNM 176569, 4(108–142); MNMHP 5304, 3(84–173); MNMHP 5303, 5(141–162). No collection data, CAS (Indiana label), 1(184).

Argentina: Patagonia, CAS 36440, 1(130).

Bryx Herald

Bryx HERALD, 1940:52 (type-species by original designation *Bryx veleronis* Herald); 1959:468 (subgenus of *Syngnathus*). *Microsyngnathus* HERALD, 1959:468 (subgenus of *Syngnathus*, type-species by original designation *Syngnathus dunckeri* Metzelaar).

DIAGNOSIS.—Urophori characterized by a very short snout; small size (generally less than 100 mm); first epibranchial reduced or not; second hypobranchials and epibranchials reduced; frontals not reaching anteriorly past middle of lateral ethmoids; ossified epaxialis tendons present or absent; one infraorbital; two nuchal plates; pouch protecting plates present; dermal flaps present or absent; 14–17 trunk rings; 27–40 tail rings; 19–31 dorsal rays; 10–14 pectoral rays; anal fin present or absent; 10 caudal rays; 10–19 rings covered by brood pouch; 0–2 + 3–7 rings covered by dorsal fin.

DISTRIBUTION.—Ten tropical species, and one species at Islas Juan Fernández and Isla San Félix.

DISCUSSION.—*Bryx* is closely related to *Cosmocampus*, and the two were probably derived from a common ancestor.

Bryx was erected by Herald in 1940 for the sole reception of *B. veleronis*. Later, Herald (1959) transferred *B. veleronis* to *Syngnathus* and retained *Bryx* as a subgenus. In the same paper *Microsyngnathus* was erected as a subgenus, with *Syngnathus dunckeri* as type-species, and *S. arctus* and *S. coccineus* included therein. *S. hildebrandi* Herald, 1965, *S. randalli* Herald, 1965, and *S. banneri* Herald and Randall, 1972, were described as being related to, or tentatively referred to, the subgenus *Microsyngnathus* species in Herald (1965) and Herald and Randall, 1972. The species of *Bryx* and *Microsyngnathus* (and *Micrognathus balli* Fowler, 1925, and *Syngnathus darrosanus* Dawson and Randall, 1975) are separated from other syngnathids and united by shared characters given in the diagnosis above. This combination of characters defines a related lineage of syngnathids worthy of generic recognition. The type-species of *Microsyngnathus* further agrees with *Bryx veleronis* in lacking an anal fin. *Microsyngnathus* Herald, 1959, thus becomes a junior synonym of *Bryx* Herald, 1940. The subgenus *Simocampus* is proposed for those species of *Bryx* possessing an anal fin.

Key to Eastern Pacific Species of *Bryx*

1a. Anal fin present (subgenus *Simocampus*) 2
1b. Anal fin absent (subgenus *Bryx*) 4
2a. Head shorter than length of dorsal fin base .... *heraldi* n.sp.
Islas Juan Fernández and Isla San Félix
2b. Head longer than length of dorsal fin base 3
3a. Dorsal fin usually entirely on tail rings,

TABLE 2. FREQUENCY DISTRIBUTIONS OF TRUNK AND TAIL RINGS, AND DORSAL FIN RAYS IN EASTERN PACIFIC SPECIES OF *Bryx*.

	Trunk rings			Tail rings									Dorsal fin rays										
	14	15	16	33	34	35	36	37	38	39	40	41	18	19	20	21	22	23	24	25	26	27	28
heraldi	—	18*	—	—	—	—	2	10	6*	—	—	—	—	—	—	—	10*	8	—	—	—	—	—
arctus	1	31*	20	—	—	—	3	5	10	18*	19	1	4	19	10*	10	9	2	—	—	—	—	—
coccineus	1	11*	1	—	—	—	1	3	2	5*	2	—	—	8*	4	—	—	—	—	—	—	—	—
veleronis	1	16*	—	2	—	1	9*	5	—	—	—	—	—	—	—	—	1	1*	1	3	4	4	2
clarionensis	—	9*	—	—	—	3	6*	—	—	—	—	—	—	—	—	—	—	—	—	1	2	4*	2

* Primary type.

except in some southern California specimens with the dorsal on a fraction of a trunk ring; 18–23 dorsal rays; double row of dark spots on trunk .... *arctus* (Jenkins and Evermann)

Tomales Bay, California, and San Felipe, Gulf of California, to Mazatlán, Mexico

3b. Dorsal fin always on at least a fraction of last trunk ring; 18–20 dorsal rays; no double row of dark spots on trunk.. *coccineus* (Herald)

Banderas Bay, Mexico, to Punta Aguja, Peru, and Galápagos Islands

4a. Snout longer than postorbital length .... *clarionensis* n.sp.

Clarión Island, Revillagigedo Islands, Mexico

4b. Snout shorter than postorbital length .... *veleronis* Herald

Galápagos and Revillagigedo Islands, and coasts of Panama and Costa Rica

Simocampus n.subgen.

TYPE-SPECIES.—*Siphostoma arctum* Jenkins and Evermann.

DIAGNOSIS.—A *Bryx* with anal fin.

INCLUDED SPECIES.—*B. arctus* (Jenkins and Evermann); *B. coccineus* (Herald); *B. balli* (Fowler); *B. banneri* (Herald and Randall); *B. hildebrandi* (Herald); and *B. darrosanus* (Dawson and Randall).

ETYMOLOGY.—From the Greek *simos*, pug-nosed, and *campos*, sea-creature.

Bryx (Simocampus) heraldi n.sp.

(Figure 5C)

DIAGNOSIS.—A *Bryx* with 22–23 (22) dorsal rays; 11 pectoral rays; 3 anal rays; 15 trunk rings; 36–38 (37) tail rings; 52–54 total rings; dorsal on 0–1 + 5.2–6 rings; 17–18 rings covered by brood pouch; head 10.3–12.3 in SL; dorsal fin base 0.8–1.0 in head; snout 2.4–2.8 in head; maximum known size 99.8 mm SL; smallest mature male 70 mm SL. See Tables 2 and 3 for additional counts and measurements.

DESCRIPTION.—All ridges of head and body moderately developed and smooth. Prenuchal and nuchal ridges elevated and easily discernible. Opercular ridge extends posteriorly about half length of opercle. Snout ridge moderately developed, extending posteriorly to interorbit. Ridges of pectoral cover plate obsolete. Trunk and tail ridges low but easily visible. Superior

TABLE 3. NUMBER OF SPECIMENS (N) AND STANDARD LENGTH RANGE, TOGETHER WITH RANGE AND MEAN ($\bar{x}$) OF SELECTED CHARACTERS EXPRESSED IN THOUSANDTHS OF STANDARD LENGTH IN *Bryx*.

		Head length		Snout length		Snout depth		Body depth		Dorsal base length		Pectoral fin length		
Species	SL	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	N
heraldi	70–100	81–97	89	29–37	33	12–16	14	29–38	34	91–113	100	16–21	18	7
coccineus	50–116	90–115	100	35–42	38	12–22	16	30–47	36	72–82	77	12–22	18	7
arctus	62–88	84–99	92	23–41	33	12–17	15	35–48	41	80–87	83	11–23	17	11
veleronis	37–49	96–113	104	41–44	43	16–19	17	35–44	38	108–130	123	17–24	20	7
clarionensis	38–50	119–131	125	39–44	42	15–20	17	36–45	40	121–136	126	23–28	25	8

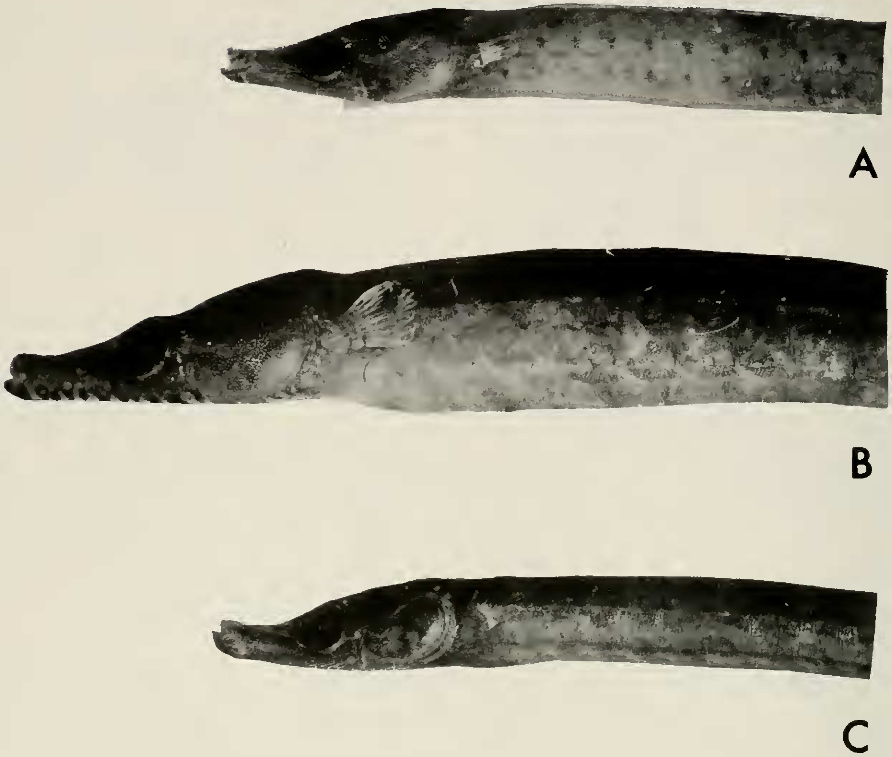

FIGURE 5. Anterior part of body of three species of eastern Pacific Syngnathidae. (*A*) *Bryx arctus*, an 88-mm-SL female, SIO H46-65. (*B*) *Bryx coccineus*, a 116-mm-SL female, USNM 220970. (*C*) *Bryx heraldi*, holotype, SIO 65-626.

tail ridge and lateral trunk ridge overlap on one plate. Scutella indistinct and about one-fourth as deep as adjoining plates. Lateral line consisting of 2–4 papillae per plate. No dermal flaps.

Protecting plates of brood pouch weakly developed; pouch folds lightly scalloped. Eggs 0.5 mm in greatest diameter, arranged in two layers four across. Males with eggs and young have been taken in early to mid-December.

Caudal fin short, as long as last two tail rings.

Coloration in alcohol. Background a light tan with few to many dark blotches on body, which, in some individuals, may make the fish appear darker brown. The dark blotches may be lighter centrally, and they may appear as dark bands 2–4 rings wide, or as thin bands between light tan areas. Brown freckling may also occur dorsally. All fins are colorless. The head coloration is essentially like that of the rest of the body. Pigmented part of cornea a darkish tan ring with radially arranged light blotches.

HABITAT.—Rocky reefs and sandy bottoms at depths of 6–23 m.

COMPARISONS.—*B. heraldi* is most closely related to *B. coccineus* and *B. arctus* of the eastern Pacific. It differs from *coccineus* is having a shorter head (10–13 rather than 8.6–11.1 in SL), 22–23 rather than 19–20 dorsal rays, and a longer dorsal fin base (0.8–1.0 rather than 1.1–1.4 in head length); and from *arctus* in lacking the double row of dark spots on the trunk and dermal flaps, and in having fewer tail rings (36–38 rather than 36–41).

RANGE.—Islas Juan Fernández and Isla San Félix.

ETYMOLOGY.—Named in honor of the late Earl S. Herald in recognition of his life-long interest in pipefish.

MATERIAL EXAMINED.—**Holotype:** SIO 65-626, a 99.8-mm-SL mature male collected from a rock ledge at Isla San Félix, Chile, from a depth of 9–12 m, with emulsified rotenone and SCUBA on 6 Dec. 1965 by Wayne Baldwin and party.

Paratypes: SIO 65-626, 2(79–82) taken with the holotype. SIO 65-624, 1(85); Isla San Félix, 9 m. SIO 65-634, 1(77); Cumberland Bay, Isla Juan Fernández, 6–11 m. GCRL 15755, 1(70); Isla Juan Fernández, 20–23 m. SIO 65–655, 1(72); Carvajal Bay, Isla Juan Fernández, 9–12 m. All taken 5–15 Dec. 1965 with emulsified rotenone and SCUBA by Wayne Baldwin and party.

Bryx (Simocampus) arctus (Jenkins and Evermann)

(Figures 5*A*, 6, 16*B*)

Siphostoma arctum Jenkins and Evermann, 1888:137 (original description; Guaymas, Sonora, Mexico; holotype USNM 39369); Jordan and Evermann 1896:771 (description).

Syngnathus arctus: Ulrey and Greeley 1928:42 (synonymy; range); Ulrey 1929:6 (Lower California; Gulf of California); Jordan, Evermann, and Clark 1930:242 (range); Starks and Morris 1907:185 (range); Hubbs 1916:160 (eelgrass; San Diego, California); Ulrey 1932:77 ("costa occidental y Golfo de California"); Herald 1940:60 (synonymy); 1959:468 (placed in subgenus *Microsyngnathus*); Feder, Turner, and Limbaugh 1974:128 (in coralline algae under kelp beds); Miller and Lea 1972:89 (description; range).

Syngnathus arcta: Berry and Perkins 1965:668 (larvae in California Current).

Diagnosis.—A *Simocampus* with 18–23 (19) dorsal rays; 3 anal rays; 9–11 pectoral rays; 14–16 (15) trunk rings; 36–41 (39–40) tail rings; dorsal on 0–0.8 + 5–5.3 rings; 17–23 rings covered by brood pouch; head 10.1–13.2 in SL; dorsal fin base 1.0–1.2 in head; snout 2.4–4.0 in head; maximum known size 121 mm SL; smallest sexually mature male 59 mm SL. See Tables 2 and 3 for additional counts and measurements.

Description.—Ridges of trunk and tail distinct and smooth. Prenuchal and nuchal ridges smooth, not separated by an indentation. Opercular ridge distinct and about half length of opercle. Snout ridge elevated and smooth from interorbital to tip of vomer. Supraorbital ridge extends posteriorly to center of opercle. Pectoral cover-plate ridges joined to form an anteriorly directed semicircle. Dermal flaps often present at junction of plates along ridges.

Protecting plates of brood pouch moderately developed; edges of pouch folds slightly scalloped. Eggs 0.5 mm in greatest diameter, arranged in two layers four across. Males with eggs and young taken from May to July.

Coloration in alcohol. Variable light tan to dark brown. May be uniformly colored or variously mottled with light and dark. Usually a double row of dark spots on sides of trunk. When patterned, background color is usually light, with dark bands on about every fourth ring. Northern fish usually darker and not mottled (Starks and Morris 1907).

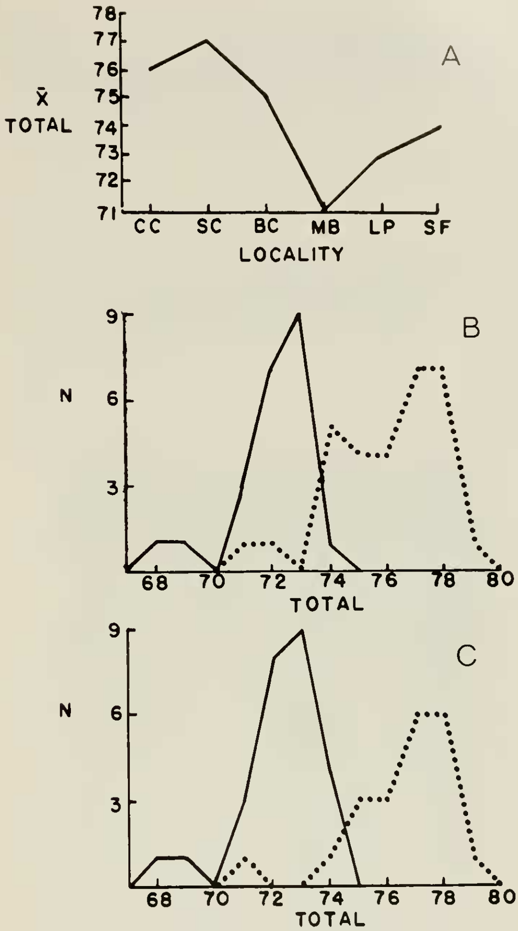

Figure 6. Clinal variation of *Bryx* (*Simocampus*) *arctus*. (*A*) Mean number of dorsal rays plus total rings plotted against locality. CC = central California; SC = southern California; BC = Baja California south of Bahía Sebastián Vizcaíno; MB = Bahía Magdalena; LP = La Paz to Bahía de Los Ángeles; SF = San Felipe. (*B*) Number of dorsal rays plus total rings; northern Gulf of California specimens included with southern specimens. (*C*) Number of dorsal rays plus total rings; northern Gulf of California specimens included with southern specimens. Dotted line indicates specimens from the north; solid line indicates specimens from the south.

Habitat.—Shallow water, 0–10 m, in bays in eelgrass, and on reefs in clumps of algae, often coralline.

Variation.—Meristic features: There are significant differences ($P \ll .001$) in mean numbers of trunk rings, tail rings, and dorsal rays between populations from the Gulf of California and central California. The differences are produced by the clinal decrease in number of rings and dorsal rays from north to south (Fig. 6). It seems reasonable to attribute this cline to the direct effect of the environmental temperature.

Comparisons.—*B. arctus* is most closely related to *B. coccineus* and *B. heraldi* in the eastern Pacific and *B. hildebrandi* in the western Atlantic. *B. arctus* can be distinguished from *B. coccineus* and *B. heraldi* by the characters given in the key and in the descriptions of these species. *B. arctus* can be distinguished from *B. hildebrandi* by the lower number of trunk rings (14–16 rather than 17), the higher number of tail rings (36–41 rather than 33–34), and the smaller head (10.1–13.7 rather than 9.5–10.7 in SL) in the former.

Range.—Tomales Bay, California, south to Mazatlán, Mexico, and throughout the Gulf of California.

Material Examined.—**California:** Tomales Bay, SU 36445, 1(74); Elkhorn Slough, CAS 45064, 1(84); SIO H45-53, 1(52). Santa Monica, UCLA W49-112, 1(60). San Pedro, SIO 74-120, 1(85); Santa Catalina Island, SIO 53-185, 2(58–79). Newport Bay, SIO H45-70, 7(70–84). San Clemente, SIO 55-73A, 2(90–94). La Jolla, SIO 58-504, 1(73); SIO H45-32, 1(85).

Outer Coast of Baja California: Bahía de Todos Santos, SIO 62-475, 1(111). Bahía San Quintín, SIO 63-1055, 3(119–121). Bahía Playa María, SIO 52-168, 1(96). Punta San Rosarito, SIO 52-162, 3(76–88). Laguna San Ignacio, SIO H50-71, 2(59–60). Bahía Santa María, SIO 62-734, 1(102). Bahía Magdalena, SIO 62-726, 7(54–91); SIO 58-61, 1(97).

Gulf of California: Isla San José, SIO 65-265, 1(62). Bahía San Carlos, CAS 48976, 4(71–84). Isla Santa Cruz, SIO 74-124, 1(59); Isla Ildefonso, SIO 65-330, 1(68). Bahía de los Ángeles, SIO 61-185, 2(90–98). San Felipe, SIO 72-79, 4(66–81). Isla Tiburón, UCLA W56-26, 2(60–67).

Sonora: Bahía, Bocochibampo, SIO 70-84, 1(79). Guaymas, USNM 39639, 1(88), holotype.

Bryx (Simocampus) coccineus (Herald)

(Figure 5*B*)

Syngnathus coccineus Herald, 1940:57 (original description; Charles Island, Galápagos Islands; holotype, USNM 101688); Fowler 1944:496 (Galápagos Islands).

Syngnathus independencia Hildebrand, 1946:153 (original description; Bahía Independencia, Peru; holotype, USNM 127853); Koepcke 1962:200 (range); Chirichigno-F. 1974:89, 351 (diagnosed in key; range).

Diagnosis.—A *Simocampus* with 19–20 (19) dorsal rays; 2–3 anal rays; 10–11 pectoral rays; 14–16 (15) trunk rings; 36–40 (39) tail rings; 51–54 total rings; dorsal on 0–1 + 4.5–5 rings; 14–16 rings covered by brood pouch; head 8.6–11.1 in SL; dorsal fin base 1.1–1.4 in head; snout 2.3–3.0 in head; maximum known size 124 mm SL; smallest sexually mature male 78 mm SL. See Tables 2 and 3 for additional counts and measurements.

Description.—All ridges of trunk and tail moderately developed. Prenuchal, nuchal, supraorbital, and snout ridges well developed. Opercular ridge one-half length of opercle on smaller specimens, becoming one-third length of opercle with growth. Two horizontal ridges on pectoral cover plate, becoming obsolete with growth. Superior tail ridge and lateral trunk ridge overlap for 0–1 plate. Lateral line with 3–6 papillae per plate. Dermal flaps may be present.

Protecting plates of brood pouch weakly developed and no deeper than one-half depth of adjacent tail; edges of pouch folds smooth to weakly scalloped. Eggs 0.6 mm in greatest diameter, arranged in one layer two or three across. Males with young have been taken at the Galápagos Islands in January. Brooding males have been collected in July in Panama.

Caudal fin as long as last four tail rings.

Coloration in alcohol. Coloration in *B. coccineus* is very variable. Background color varies from a light tan to dark brown. Specimens may be a uniform light tan to dark brown, or more usually, light with darker markings. Light tan specimens may have darker spots at the bases of the dorsal rays and pectoral rays. The specimens with tan background and darker blotches do not have any unifying color pattern. One specimen has the venter dark brown and dorsum light tan, with dark bands extending over the dorsum on every three or four rings. Many specimens, however, have a whitish blotch on the pectoral cover plate and immediately posterior to the orbit. Hyoid region may be dark with a series of whitish spots.

Habitat.—Beds of red algae and coral heads at depths from 0–18 m.

Comparisons.—*B. coccineus* is most closely related to its eastern Pacific congeners *B. heraldi* and *B. arctus*. *B. coccineus* differs from the former by the characters discussed in the description of *B. heraldi*, and from the latter in lacking the double row of dark spots on the trunk and in having a longer head (8.6–11.1 rather than 10.1–13.2 in SL). Examined type material of *S. independencia* agrees in all respects with the holotype of *B. coccineus*. It is likely that the exceptional occurrence of *B. coccineus* in Independencia Bay, Peru, in 1941 was the result of transport of individuals southward during the extreme El Niño of that year (Lobell 1942).

Range.—Bahía Banderas, Mexico, to Punta Aguja, Peru (occasionally to Bahía Independencia), and the Galṕagos Islands.

Material Examined.—**Mexico:** Bahía de Banderas, SIO 62-42, 1(116).

Costa Rica: Puerto Culebra, USNM 101690, 1(57). Puerto Jimenez, USNM 92120, 1(50). Both paratypes of *S. coccineus*.

Panama: Isla Canal de Afuera, SIO 71-52, 1(65).

Peru: 6°55′S, 80°42′W, USNM 220970, 1(116). Bahía Independencia, USNM 127853, 1(124), holotype of *S. independencia*; USNM 127854, 2(88–108), paratypes of *S. independencia*.

Galápagos Islands: Isla Santa María, USNM 101688, 1(87), holotype of *S. coccineus*. Isla Fernandina, USNM 220971, 6(62–98); USNM 220972, 1(77).

Subgenus **Bryx** Herald

Type-species.—*Bryx veleronis* Herald.

Diagnosis.—A *Bryx* without an anal fin.

Included Species.—*B. veleronis* Herald; *B. clarionensis* n.sp.; *B. dunckeri* (Metzelaar); *B. randalli* (Herald).

Bryx (Bryx) veleronis Herald

(Figures 7*B* & 8)

Bryx veleronis Herald, 1940:55 (original description; Albemarle Island, Galápagos Islands; holotype LACM 20012).

Diagnosis.—A *Bryx* with 22–28 dorsal rays; 11–13 pectoral rays; 14–15 trunk rings; 33–37 tail rings; 48–52 total rings; dorsal on 0–0.5 + 5.5–7.0 rings; 11.5–15 rings covered by brood pouch; head 8.3–10.3 in SL; dorsal fin base 0.8–1.0 in head; snout 1.2–1.5 in postorbital; maximum known size 60 mm SL; smallest sexually mature male 45 mm SL. See Figure 8, and Tables 2 and 3 for additional counts and measurements.

Description.—Ridges of trunk and tail moderately developed, serrate and with an indentation at plate junctions. Prenuchal and nuchal plates with sharply defined serrate ridge. Snout ridge well developed, wholly on mesethmoid. Opercular ridge three-fourths length of opercle. Supraorbital ridge weak. Two parallel horizontal ridges on pectoral cover plate. Superior tail and median trunk ridges overlap for one ring. Scutella indistinct and half as deep as adjoining plates. Lateral line consisting of 1–2 papillae per plate. Dermal flaps may be present, especially on upper surface of head.

Figure 7. Anterior part of body of three species of eastern Pacific Syngnathidae. (*A*) *Bryx clarionensis*, holotype, SIO 74-116. (*B*) *Bryx veleronis*, a 34-mm-SL female, SIO 67-40. (*C*) *Hippocampus ingens*, in life.

Protecting plates of brood pouch weakly developed and no deeper than half depth of adjacent plate; edges of pouch folds smooth. Eggs 0.5–0.75 mm in greatest diameter, arranged in one layer two across. Males with young taken in July.

Coloration in alcohol. Body a light to dark tan, with various amounts of mottling, but no definite pattern. Opercular membrane and hyoid region may be brownish, with white spots and bars almost serially arranged. Pectoral and dorsal fins clear, caudal colored the same as rest of body. Body may have sprinkling of punctate melanophores ventrally. One or two brownish streaks may extend posteriorly from orbit.

HABITAT.—In red-algae beds and coral heads at depths of 3–18 m.

COMPARISONS.—Most closely related to *B. clarionenesis*. For further comparisons see discussion under that species.

RANGE.—Taken only at islands, including the Galápagos Islands; Islas Revillagigedo; Isla Murciélago and Isla del Caño, Costa Rica; and Islas San José and Canal de Afuera, Panama.

MATERIAL EXAMINED.—**Islas Revillagigedo:** Isla Clarión, LACM 20013 (formerly AHF VELERO sta. 305-34), 13(45–49), paratypes. Isla Socorro, UCLA W55-124, 1(41).

Costa Rica: Isla del Caño, LACM 31579-15, 6(37–48).

Panama: Archipiélago de las Perlas, SIO 67-38, 1(37); SIO 67-40, 1(34). Isla Canal de Afuera, SIO 71-52, 1(46).

Galápagos Islands: Isla Santa María, USNM 101689, 1(48), paratype.

Bryx (Bryx) clarionensis n.sp.

(Figures 7*A* & 8)

DIAGNOSIS.—A *Bryx* with 25–28 dorsal rays; 11–13 pectoral rays; 15 trunk rings; 35–36 tail rings; 50–51 total rings; dorsal on 0–1 + 6–7 rings; head 7.6–8.4 in SL; dorsal fin base 0.9–1.1 in head; snout 0.8–0.9 in postorbital; maximum known size 47 mm SL; males unknown. See Figure 8, and Tables 2 and 3 for additional counts and measurements.

DESCRIPTION.—All ridges of head and body distinct and moderately serrate. Prenuchal and nuchal ridges slightly elevated. Opercular ridge extends posteriorly for entire length of opercle. Snout ridge extends from interorbital region to anterior end of mesethmoid. Pectoral cover plate with two obsolete horizontal ridges. Trunk and tail ridges not markedly indented between rings. Superior tail and lateral trunk ridges do not overlap. Scutella small, indistinct. Lateral line not visible. Many cirruslike dermal flaps on dorsal surface of head in a few specimens.

Coloration in alcohol. Background color orangish tan, with a series of light and dark bands in a few specimens, each about two rings in width around tail. Brown frecklelike spots may appear on dorsal surface of head and along sides of snout. Abdominal region slightly darker than rest of body. Dorsal and pectoral fins colorless, caudal rays orangish brown.

HABITAT.—Known only from the types taken at the surface near Isla Clarión, Mexico.

COMPARISONS.—*B. clarionenesis* differs from the closely related species *B. veleronis* in having a longer snout (0.8–0.9 rather than 1.4–1.5 in postorbital) and the snout ridge not quite so elevated and serrate. Figure 8 provides a comparison of the snout length versus standard length for each species. Both species have been collected at Isla Clarión.

RANGE.—Isla Clarión, Islas Revillagigedo, Mexico.

ETYMOLOGY.—Named for the type-locality.

MATERIAL EXAMINED.—**Holotype:** SIO 74-116, formerly UCLA W55-136, a 47-mm-SL mature female dip-netted under a night light over 15 fathoms (27 m) at the SE anchorage, Isla Clarión, 20 Apr. 1955, by John Fitch, Wayne Baldwin, and B. Craig.

Paratypes: SIO 74-116, 7(38–50), and GCRL 15754, 1(41), same data as holotype.

Syngnathus Linnaeus

Syngnathus LINNAEUS, 1758:336 (type-species by Int. Comm. Zool. Nom. Opinions 45 and 77: *Syngnathus acus* Linnaeus); DUNCKER 1912:236 (description); 1915:78 (description; subgenera); JORDAN, EVERMANN, AND CLARK 1930:240 (North American species; synonymy); HERALD 1943:141 (in part; description; subgenera).

Siphostoma RAFINESQUE, 1810:18 (type-species by monotypy, *Syngnathus pelagicus* Linnaeus); JORDAN AND EVERMANN 1896:761 (description; synonymy).

Siphonostoma KAUP, 1853:233 (emmendation of *Siphostoma*); 1856:48 (description).

Dermatostethus GILL, 1863:283 (type-species by monotypy, *Dermatostethus punctipinnis* Gill [=*Syngnathus acus* Linnaeus]); JORDAN, EVERMANN, AND CLARK 1930:240 (range).

Syrictes JORDAN AND EVERMANN, 1927:504 (type-species by original designation, *Syngnathus fuscus* Storer).

DIAGNOSIS.—Syngnathids with subcaudal brood pouch protected by plates; nuchal and prenuchal plates and scutella present; superior ridges of trunk and tail discontinuous; lateral ridge of trunk and superior ridge of tail continuous or subcontinuous; inferior trunk and tail ridges continuous; opercular ridge present or re-

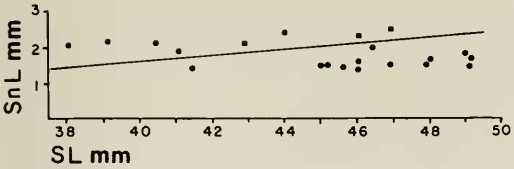

FIGURE 8. Comparison of snout length plotted against standard length for *Bryx veleronis* (closed circles) and *Bryx clarionensis* (closed squares).

duced to only basal part; pectoral, dorsal, anal, and caudal fins developed; dorsal fin base not raised; first hypobranchial reduced to absent; remainder of branchial skeleton present, without tooth plates; jugular plates well developed, separated by a median plate; body ridges generally smooth to finely serrate, both neither strongly toothed nor serrate; 2–3 infraorbitals; 25–47 dorsal rays; 2–4 anal rays; 11–14 pectoral rays; 10 caudal rays; 14–23 trunk rings; 33–50 tail rings. This genus contains some of the largest species in the family; *S. californiensis* reaches a length of 533 mm SL. Marine and fresh water, cosmopolitan, but most abundant in temperate seas.

DISCUSSION.—Herald (1943, 1959), following the preliminary analysis of Duncker (1915), divided the genus into four subgenera differentiated on the basis of brood-pouch closure. On osteological grounds, I conclude that two of these subgenera (*Bryx* and *Microsyngnathus*) together constitute a distinct genus (*Bryx*). *Syngnathus* is the most speciose pipefish genus, with perhaps 40 species.

Key to Eastern Pacific Species of *Syngnathus*

1a. Trunk rings 14–16 ($\bar{x}$ = 15) .... *auliscus* (Swain)
Santa Barbara Channel, California, to northern Peru; in eelgrass of bays and sloughs

1b. Trunk rings 17 or more (6 of 914 specimens of *S. leptorhynchus* have 16) 2

2a. Snout long, compressed, usually contained less than 1.8 in head length 3

2b. Snout shorter, round, usually contained more than 1.8 times in head length........ 5

3a. Total rings fewer than 63; all ridges of trunk and tail distinctly keeled............. *carinatus* (Gilbert)
Northern Gulf of California

3b. Total rings more than 63; all ridges of trunk and tail rounded 4

4a. Total rings 63 or more, usually 64–66; 35–41 dorsal rays, usually 37–40 (see Fig. 11), dark bar extending diagonally from orbit across opercle .... *exilis* (Osburn and Nichols)
Halfmoon Bay, California, to Bahía Magdalena, Baja California; on sand bottoms

4b. Total rings 67–72, usually 68–70; 39–48 dorsal rays, usually 42–46 (see Fig. 11), no dark bar across opercle .... *californiensis* Storer
Bodega Bay, California, to Bahía Santa María, Baja California; associated with kelp beds, often epipelagic

5a. Pectoral fins long, extending posteriorly across two full trunk rings.................... *macrobrachium* n.sp.
Tumbes, Peru, to Puerto Montt, Chile

5b. Pectoral fins short, never extending posteriorly across two full rings 6

6a. Total rings more than 60 7

6b. Total rings 60 or fewer 8

7a. Trunk length 1.5 or more in tail length; total rings 60–68; dorsal rays 33–45 .... *euchrous* n.sp.
Redondo Beach, California, to Bahía de Ballenas, Baja California; near bottom off rocky shores

7b. Trunk length 1.5 or less in tail length; total rings 53–64; dorsal rays 28–43 .... *leptorhynchus* Girard (in part)

8a. Interorbital 3 in postorbital; head usually more than 8.6 in SL .. *leptorhynchus* Girard
Southeastern Alaska to Bahía Santa María, Baja California; in eelgrass of bays

8b. Interorbital more than 3 in postorbital; head usually less than 8.6 in SL.................... *insulae* n.sp.
Isla Guadalupe, Mexico, in algae and eelgrass, 20–34 m

Syngnathus auliscus (Swain)

(Figures 4D & 9)

Siphostoma auliscus SWAIN, 1882:547 (original description; Santa Barbara and San Diego, California; types lost); JORDAN AND GILBERT 1883:905 (description; range); SWAIN AND MEEK 1884:238 (diagnosed in key); JORDAN AND EVERMANN 1896:767 (description; range); EIGENMANN AND EIGENMANN 1892:144 (San Diego).

Syngnathus auliscus: STARKS AND MORRIS 1907:184 (range); HUBBS 1916:160 (description); ULREY AND GREELEY

TABLE 4. FREQUENCY DISTRIBUTIONS OF TRUNK AND TAIL RINGS, AND DORSAL FIN RAYS IN EASTERN PACIFIC SPECIES OF *Syngnathus*.

	Trunk rings									Tail rings																		
	14	15	16	17	18	19	20	21	22	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
auliscus	17	56	16	—	—	—	—	—	—	1	16	19	23	20	10	—	—	—	—	—	—	—	—	—	—	—	—	—
carinatus	—	—	7	57*	1	—	—	—	—	—	—	—	—	—	1	6	22	33	3	—	—	—	—	—	—	—	—	—
exilis	—	—	—	2	94	21	10*	1	—	—	—	—	—	—	—	—	—	—	3	10	22	33*	38	15	3	—	—	—
californiensis	—	—	—	—	—	1	20	48	6	—	—	—	—	—	—	—	—	—	—	—	—	6	10	36	25	5	2	1
macrobrachium	—	—	1	19	12	—	—	—	—	—	—	—	—	—	—	5	11	13*	3	—	—	—	—	—	—	—	—	—
euchrous	—	—	—	—	39	133*	25	—	—	—	—	—	—	—	—	—	5	27	44	37	26	33	12*	6	2	—	—	—
leptorhynchus	—	—	9	146	443	267	55	1	—	—	—	11	41	109	112	104	75	123	168	157	29	1	—	—	—	—	—	—
insulae	—	—	—	11	18	2*	—	—	—	—	—	—	—	—	—	5	10*	13	—	—	—	—	—	—	—	—	—	—

	Dorsal fin rays																						
	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
auliscus	3	13	18	23	18	6	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
carinatus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	10	10	15	11*	15	1	—	—
exilis	—	—	—	—	—	—	—	—	—	—	16	30	26	20	15	10*	2	1	—	—	—	—	—
californiensis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	6	13	9	9	13	17	5	2
macrobrachium	—	—	—	—	—	—	—	—	—	—	1	1	1	7*	5	8	3	1	2	—	—	—	—
euchrous	—	—	—	—	—	—	—	1	9	10	24	24	29	30	18	11	14*	9	6	5	—	—	—
leptorhynchus	—	—	4	18	39	50	87	76	73	58	86	98	113	99	56	30	14	2	—	—	—	—	—
insulae	—	—	—	—	—	6	7*	12	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—

* Primary type.

TABLE 5. NUMBER OF SPECIMENS (N) AND STANDARD LENGTH RANGE, TOGETHER WITH RANGE AND MEAN ($\bar{x}$) OF SELECTED CHARACTERS EXPRESSED IN THOUSANDTHS OF STANDARD LENGTH IN *Syngnathus*.

		Head length		Snout length		Snout depth		Body depth		Dorsal-base length		Pectoral-fin length		
Species	SL	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	N
auliscus	46–134	98–136	113	44–56	48	10–19	15	18–46	31	98–124	112	13–21	18	9
carinatus	116–230	113–141	128	65–89	76	8–10	9	16–26	22	114–138	127	15–26	21	17
exilis	75–238	102–148	121	50–88	68	7–13	10	20–44	29	95–120	107	13–21	16	37
californiensis	78–382	111–143	120	55–93	69	6–12	9	15–41	24	100–128	115	9–18	14	33
macrobrachium	92–190	112–144	137	60–82	72	10–14	12	26–35	30	121–140	130	21–34	29	15
euchrous euchrous	111–249	100–132	114	47–78	55	8–14	11	22–40	29	111–128	118	10–23	17	20
e. ollotropis	116–244	93–108	103	44–57	49	10–12	11	22–30	26	96–127	112	10–15	13	10
leptorhynchus	57–245	104–148	122	48–87	65	8–15	12	20–55	27	97–141	118	10–20	16	92
insulae	88–180	107–117	111	46–57	52	10–14	11	19–30	24	105–114	109	13–19	16	7

1928:42 (synonymy; range); ULREY 1929:6 (Lower California); JORDAN, EVERMANN, AND CLARK 1930:240 (range); ULREY 1932:77 (Golfo de California); BARNHART 1936:34 (description; range); HERALD 1940:60, 63 (key; synonymy; range); CASTRO-AGUIRRE ET AL. 1970:131 (not common in Gulf of California); MILLER AND LEA 1972:89 (description; range); CHIRICHIGNO-F. 1974:351 (range).

Singnathus auliscus; VAILLANT 1894:70 (Gulf of California).

Siphostoma sinaloae JORDAN AND STARKS 1896:268 (original description; Mazatlán; holotype SU 2945).

Syngnathus tweedlei MEEK AND HILDEBRAND, 1923:259 (original description; Chame Point, Panama; holotype USNM 82088).

DIAGNOSIS.—A *Syngnathus* with 26–33 (27–30) dorsal rays; 10–14 pectoral rays; 2–3 anal rays; 14–16 (15) trunk rings; 34–39 (36–37) tail rings; 0.2–1.5 + 5–7.2 rings covered by dorsal fin; total rings covered by dorsal fin 6–7.9; 15–21 pouch rings; head 7.1–10.1 in SL; dorsal fin base 0.8–1.6 in head; snout 2.0–2.8 in head; maximum known size 178 mm SL; smallest sexually mature male 71 mm SL. See Tables 4 and 5 for additional counts and measurements.

DESCRIPTION.—All ridges of body smooth, rounded, low but distinct. Prenuchal and nuchal ridges low but distinct. Opercles strongly convex, with median ridge reaching half the length. Snout ridge running full length of snout to interorbital. Head not raised at orbit, so that snout ridge almost horizontal. Supraorbital ridge originating just anterior to nostrils and ending above anterior edge of opercle. Pectoral cover plate with one obsolete ridge. Lateral trunk and superior tail ridges overlap for one ring. Slightly acute ventral trunk ridge. Three lateral line papillae per plate. Dermal flaps rarely present.

Plates protecting brood pouch well developed, often as deep as overlying tail rings. Eggs 0.6–0.7 mm in greatest diameter, arranged in two layers four across. Brooding males collected in April through August.

Fins of moderate size, caudal as long as last three tail rings. Pectoral base about 1.5 in its length.

Juveniles less than 25 mm SL (Fig. 9) are much spinier than adults. Large broad-based spine on each frontal; opercle has a broad-based lateral projection, and each ring has a well-developed spine on each ridge. Dorsal fin high. Mouth large and upturned. Body whitish with light brown pigmented spots forming a band dorsal to gut anteriorly and continuing posteriorly along ventral surface of tail. Occasionally with sprinkling of pigment spots on body, concentrated on ventral surface of gut and along dorsal base.

Coloration in life. Variations of brown or green, never red.

Coloration in alcohol. Usually light tan to brown, lighter ventrally. Median caudal rays brown; outer two rays light tan; all other fins colorless. Usually a dusky blotch below nostrils. Sometimes a brownish streak at lower-posterior corner of orbit. Often there is on the body much darker mottling, which may alternate with light areas, especially posteriorly, giving a dark-light banded appearance. Lighter bands usually narrower and separated by five to six rings.

HABITAT.—Eelgrass of bays and sloughs. Occasionally in floating *Sargassum*.

COMPARISONS.—Although *S. auliscus* is a chiefly tropical species, it occurs rather frequently in the southern part of San Diego Bay, where the temperature is raised by a thermal

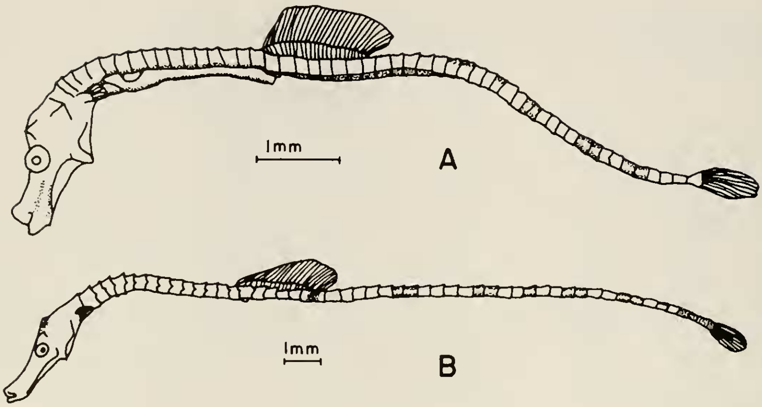

FIGURE 9. Juvenile *Syngnathus auliscus* from San Diego Bay, California. (*A*) 9.2 mm SL. (*B*) 16.3 mm SL.

effluent; this is the only place in California where this species has been found in larger numbers than other pipefishes. It may be confused in this region with the similar *S. leptorhynchus*. *S. auliscus* differs from *S. leptorhynchus* in having 14–16 trunk rings rather than 17 or more; in having a deeper and more robust trunk; and in reaching a much smaller size as adults.

RANGE.—Santa Barbara Channel, California, to Paita, Peru, and throughout the Gulf of California.

MATERIAL EXAMINED.—**California:** Newport Bay, LACM W55-257, 1(162). Peñasquitos Lagoon, SIO 73-411, 1(178). San Diego, SIO H46-94, 2(127–134); G. McGowen personal collection, 89(7.4–31.8).

Mexico: Bahía de Tortugas, SIO H48-53, 1(92). Bahía Almejas, SIO 65-181, 2(98–111). Cholla Bay, CAS 45071, 2(91–99). Puerto Peñasco, GCRL V73:10729, 2(65–82). Guaymas, R. Behrstock, personal collection, 38(29–112). Sinaloa, GCRL V71:6572, 1(123); GCRL V68:2639, 1(81): GCRL V71:6565, 2(46–52). Mazatlán, SU 2945, 1(87), holotype of *S. sinaloae*.

Nicaragua: Corinto, CAS 6346, 1(74).

Costa Rica: Puntarenas, GCRL V69:3526, 3(44–83).

Panama: Chame Point, USNM 82088, 1(71), holotype of *S. tweedlei*.

Peru: Tumbes, IMARPE uncat., 2(?–100). Paita, IMARPE uncat., 1(87).

Syngnathus carinatus (Gilbert)

(Figure 10*B*)

Siphostoma carinatum GILBERT, 1892:547 (original description; 31°31′45″N, 114°19′W; lectotype here designated as SU 240); JORDAN AND EVERMANN 1896:763 (description).

Syngnathus carinatum: BREDER 1928:24 (Isla Tiburón, Bahía Adair, San Felipe).

Syngnathus carinatus: ULREY 1929:6 (Gulf of California); JORDAN, EVERMANN, AND CLARK 1930:240 (range); ULREY 1932:77 (Golfo de California); FOWLER 1944:496 (range).

Syngnathus acus; (not of Linnaeus) HERALD 1940:60 (diagnosed in key; range).

Syngnathus griseolineatus leptorhynchus: (not of Girard) CASTRO-AGUIRRE ET AL. 1970:132 (Gulf of California).

DIAGNOSIS.—A *Syngnathus* with 40–46 (41–45) dorsal rays; 13–15 pectoral rays; 3–4 anal rays; 16–18 (17) trunk rings; 39–43 (41–42) tail rings; 56–60 total rings; dorsal on 0.1–1.8 + 7.5–11.1 rings; total rings covered by dorsal 9–12.1; 21.5–22 rings covered by brood pouch; head 7.1–8.6 in SL; dorsal fin base 0.9–1.2 in head; snout 1.6–1.8 in head; maximum known size 230 mm SL; smallest sexually mature male 182 mm SL. See Tables 4 and 5 for additional counts and measurements.

DESCRIPTION.—All ridges on body usually well developed and serrate. Supraoccipital, nuchal, and prenuchal ridges low and finely serrate. Opercular and supraorbital ridges low. Snout ridge slightly elevated and serrate, extending posteriorly to region above anterior edge of orbit. Pectoral cover plate with only superior ridge. Superior trunk ridge extending forward dorsally to gill opening and ending just below nuchal plate. Lateral trunk and superior tail ridges usually not overlapping, but may overlap for half width of last trunk ring. Scutella easily discernible, about half as deep as median trunk plate. Lateral line consisting of 6–7 papillae per plate. No dermal flaps.

Protecting plates of brood pouch well developed, more than half as high as adjacent tail; margin of folds of brood pouch smooth. Eggs 0.9–1.0 mm in greatest diameter, arranged in two layers six across. Males with eggs have been collected in November.

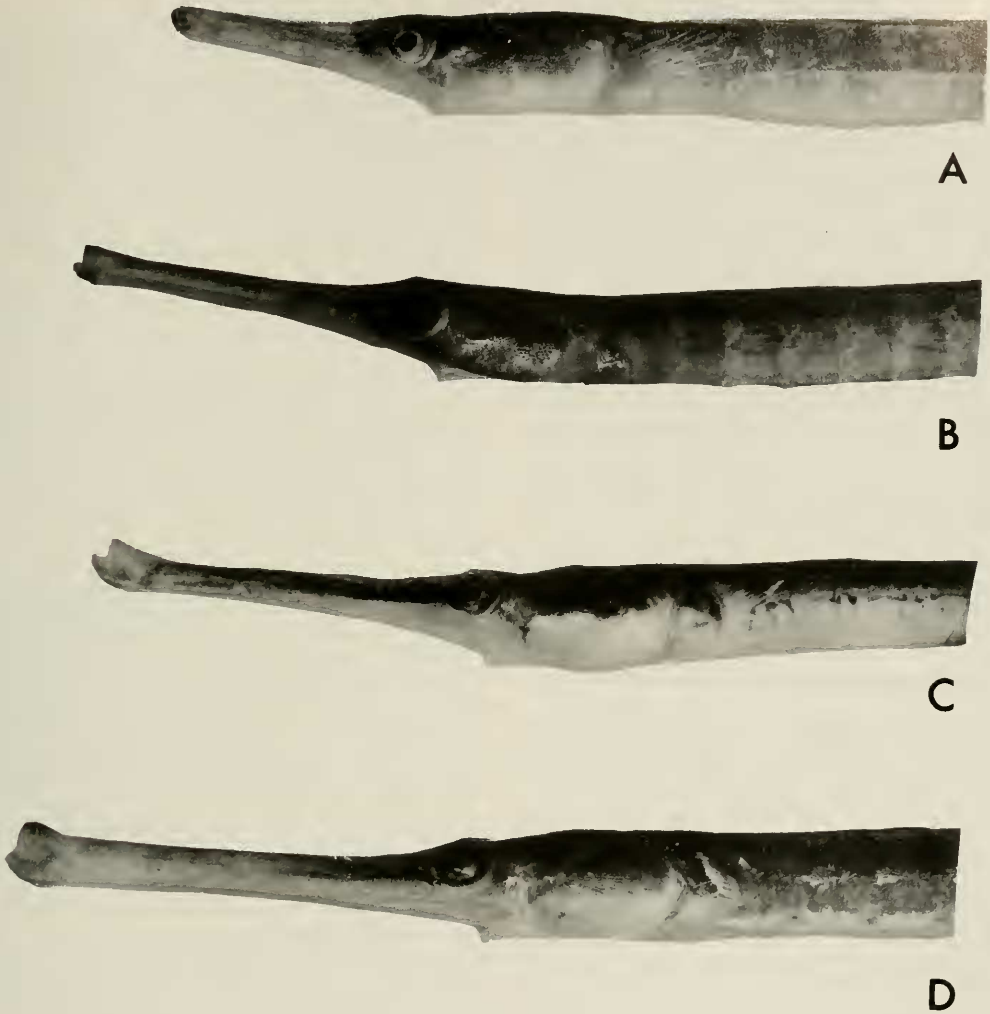

FIGURE 10. Anterior part of body of four species of eastern Pacific Syngnathidae. (*A*) *Syngnathus macrobrachium*, holotype, USNM 176501. (*B*) *Syngnathus carinatus*, a 200-mm-SL female, SIO 72-60. (*C*) *Syngnathus exilis*, a 238-mm-SL female, SIO 75-661. (*D*) *Syngnathus californiensis*, a 285-mm-SL female, SIO 62-552.

Fins all well developed. Pectoral fin extends posteriorly to edge of first trunk ring or middle of second trunk ring.

Coloration in alcohol. Older specimens a uniform light tan to dark brown, with caudal dusky and dark spots at bases of dorsal rays. Fresh specimens with immaculate white undersides becoming silvery on opercle and pectoral cover plate. Dorsum light green-brown with white areas around scutella, which may be connected by white streaks to adjacent scutella. Thus, a chainlike pattern often evident dorsolaterally. Caudal fin green-brown centrally with light edges. Snout with the same green-brown color dorsally. Other fins colorless.

MERISTIC VARIATION.—The number of trunk rings in *S. carinatus* is relatively stable, usually 17, except that three of the four specimens from Bahía Kino had 16. The same trend is shown by the number of tail rings. The normal range is from 41–42, but two of the four specimens from Bahía Kino had 40 tail rings.

COMPARISONS.— As indicated in the account of *S. macrobrachium*, *S. carinatus* is closely related to *macrobrachium*, *schlegeli*, and *folletti*. It seems to be most closely related to the

Japanese *S. schlegeli*. It differs from *schlegeli* in coloration (light coloration with chainlike pattern rather than dark brown), longer snout, and in that the superior trunk ridge is continued anteriorly above the gill opening. The relationship of *S. carinatus* to a Japanese fish parallels the distribution indicated by Dawson (1944) for some algae.

RANGE.—Northern part of Gulf of California, from head of Gulf and from Bahía San Luis Gonzaga in the west to Bahía Kino in the east.

MATERIAL EXAMINED.—Gulf of California: Mouth of Río Colorado, SIO 63-484, 2(132–139). Between El Golfo and San Felipe, S. Guevara personal collection, 20(161–216). Off Bahía Adair, BOC 1184, 11(86–148). 31°32′30″N, 114°20′W, USNM 48250, 3(185–287); USNM 127139, 2(187–189); USNM 125028, 2(178–183), paralectotypes. 31°31′45″N, 114°19′W, SU 240, 1(198), lectotype; SU 67670, 3(186–201), paralectotypes. San Felipe, SIO 72-60, 2(203–209); SIO 58-164, 1(127); SIO H47-53, 47(132–165); SIO 74-118, 3(182–230); BOC 1017, 5(81–156). Punta Diggs, UCLA W62-61, 5(131–152). Isla Willard, LACM 22298, 1(210). Isla Tiburón, BOC 1010, 1(123). Bahía Kino, SIO 60-113, 4(115–133).

Syngnathus exilis (Osburn and Nichols)

(Figures 10*C* & 11)

Siphostoma exile OSBURN AND NICHOLS, 1916:153 (original description; west San Benito Island, Baja California; holotype USNM 87543, formerly AMNH 5203).

Syrictes exilis; JORDAN, EVERMANN, AND CLARK 1930:243 (range).

Syngnathus californiensis californiensis; HERALD 1940:60 (in part); 1941:62 (in part).

Syngnathus exilis; ULREY 1929:6 (listed); MILLER AND LEA 1972:212 (range).

DIAGNOSIS.—A *Syngnathus* with 36–41 (rarely 35, 42 or 43) (37–40) dorsal rays; 11–14 pectoral rays; 3 anal rays; 17–21 (18) trunk rings; 43–49 (rarely 50) (45–47) tail rings; 63–68 (64–66) total rings; dorsal on 0–1.9 + 7–9.5 rings; brood pouch covering 19–26 rings; head 6.8–9.8 in SL; dorsal fin base 0.9–1.4 in head; snout 1.6–2.0 in head; eggs 1.0–1.2 mm in greatest diameter, arranged in two layers four across. Maximum known size 253 mm SL; smallest sexually mature male 125 mm SL. See Tables 4 and 5 for additional counts and measurements.

DESCRIPTION.—Ridges of trunk and tail smooth and rounded. Nuchal and prenuchal ridges obsolete to absent, smooth. Opercular ridge distinct, reduced to basal third of opercle. Snout ridge low, smooth to slightly serrate, reaching from vomer to anterior part of interorbital; slightly elevated posteriorly. Superior ridge of pectoral cover plate absent, inferior ridge obsolete. Lateral trunk and superior tail ridges overlap on first tail ring. Trunk and tail ridges smooth to slightly rugose. Scutella small, about one-third as deep as adjoining plates. Snout moderately compressed. Abdomen typically and rather distinctly with posterior swelling, especially in juveniles and females. Lateral line consisting of 4–5 papillae per plate. Often with a pair of stitches on first trunk ring and nuchal plates. No dermal flaps.

Pouch protecting plates well developed, about as high as adjacent tail. Eggs 1.0–1.2 mm in greatest diameter, arranged in two layers four across. Brooding males found throughout year.

Pectoral fins reach posteriorly to just past junction of first and second trunk rings. Caudal fin as long as last three tail rings.

Coloration in life. From C. L. Hubbs's field notes for SIO H47-43.

The specimens become sooty toward the caudal. Of the half grown, one is blackish green the other tan, much variegated with lighter and darker. All are much speckled with light on top of head. The female varies from greenish brown anteriorly to reddish brown posteriorly. The male is brown, becoming orange toward the brood pouch. The lower part of the opercle of all is silvery with a more or less distinct dark stripe behind the lower part of the eye. Dark markings on lower part of opercle are incipient. All but the adult male have a diffuse dark streak on belly. The adults show the half crescents on the body just above the ventrolateral keel. The adult male is rather conspicuously banded with light. The others indefinitely so.

Coloration in alcohol. The most striking feature of alcoholic specimens is the dusky stripe on the snout extending from the nostrils anteriorly on the greater part of the snout, and the bar that courses diagonally from the posteroventral margin of the orbit to the opercle. These markings may be wanting in older specimens. The general body color is typical for most species of *Syngnathus*; i.e., a ground color tan to dark brown, with various mottlings of darker brown.

HABITAT.—On the bottom off sandy beaches, often associated with pieces of detached algae. Occasionally, juveniles are taken in the plankton, sometimes associated with flotsam. Two specimens (SIO H51-203 and CAS 32983) were taken from the guts of albacore (*Thunnus alalunga*).

COMPARISONS.—*S. exilis* is a long-snouted pipefish of the outer coast, resembling *S. californiensis* in general appearance. It can be distinguished from that species by its smaller size at maturity, generally fewer trunk rings ($\bar{x}$ = 18.3 vs $\bar{x}$ = 20.8), coloration (especially the presence of the dark oblique bar at the posterior corner of the orbit), the abdomen usually with a posterior swelling, and the sand-bottom vs kelp-bed habitat. Figure 11 provides information for easy separation of *S. exilis* from *S. californiensis*.

RANGE.—Half Moon Bay, California, to Bahía Magdalena, Baja California, including the channel islands of California and Isla Guadalupe, Mexico.

MATERIAL EXAMINED.—**California:** Half Moon Bay, SIO 54-106, 1(217). Guide Seamount, CAS 32983, 1(97). Del Monte Beach, SIO 74-195, 2(92–196). Monterey, CAS 27950, 1(89). San Luis Obispo, SIO 55-35, 1(164); SIO H50-195, 2(217–227). Los Angeles, SCCWRP sta. T_1-75, 4(176–199); SCCWRP sta. T-0, 4(132–203). Long Beach, UCLA W50-128, 2(228–235). Newport Beach, SIO H45-70, 17(120–239). Dana Point, SCCWRP sta. Fv. 3, 5(105–190). Torrey Pines Lagoon, UCLA W63-49, 2(170–175). La Jolla, SIO H47-43, 4(96–163); SIO H47-106, 48(107–242); SIO H51-153, 13(136–227); SIO H46-63, large series; SIO H47-158, 34(96–225); SIO H47-134, 1(170); SIO H48-163, large series. Santa Cruz Island, SIO H51-259, 1(115). Santa Catalina Island, LACM 30510-9, 1(85); LACM 30865-3, 1(42). Mission Bay, SIO 61-412, 1(113); San Diego Bay, SIO H50-112, 1(219).

Baja California: Islas Coronados, SIO H46-125, 1(145). Punta Banda and Isla de Todos Santos, SIO 61-284, 1(120); SIO 68-302, 1(160); SIO H51-24, 2(102–118). Punta Santo Tomas, SIO 65-440, 1(103). Cabo Colnett, SIO H51-303, 1(181); CAS 3295, 8(114–161). Bahía San Quintín, SIO H50-25, 1(239); SIO 60-453, 1(135). Bahía San Carlos, SIO H52-210, 4(114–247). Bahía Blanca, SIO 60-327, 3(158–250). Bahía Playa María, SIO H52-169, 2(120–224). Isla Guadalupe, SIO 65-72, 1(130). Bahía Santa Rosalía, SIO 62-282, 1(164). Bahía Sebastián Vizcaíno, SIO H52-135, 9(131–228). Islas San Benitos, USNM 87534, 1(166), holotype. Isla Cedros, SIO 68-345, 1(175); UCLA W60-126, 1(123); SU 67915, 1(117); SIO 65-591, 1(220); SIO 62-756, 1(145); SIO H53-110, 1(193). Punta Eugenia, SIO 61-398, 1(70). Cabo Tortolo, SIO H48-55, 1(180). Bahía Tortugas, SIO H48-51, 1(98); SIO 63-806, 1(141); SIO 59-25, 1(155); SIO H48-33, 3(192–238); SU 2488, 1(123); AMNH 5588, 5(99–118), paratypes. Bahía San Roque, SIO 63-16, 1(84); SIO 64-185, 1(152). Bahía Asunción, SIO 68-303, 1(161); SIO 62-535, 2(100–110); SIO 68-301, 2(96–151); SIO H51-96, 1(174); SIO H48-92, 1(115); SIO 66-147, 1(190); SIO 64-68, 3(161–226). Bahía San Hippolito, SIO 64-750, 14(70–253). Bahía de Ballenas, SIO 64-405, 1(173); SIO 64-765, 1(180); SU 767, 1(147). Bahía Santa María, SIO H50-149, 1(136). Bahía Magdalena, SIO H50-96, 1(67).

Syngnathus californiensis Storer

(Figures 10*D*, 11, 16*C*)

Syngnathus californiensis STORER, 1848:73 (original description; California; holotype lost); STARKS AND MORRIS 1907:183 (meristic features); STARKS 1911:177 (not included in Puget Sound fauna); HUBBS 1916:158 (description); 1921:4 (range; counts); ULREY AND GREELEY 1928:42 (synonymy; range); ULREY 1929:6 (included in list); JORDAN, EVERMANN, AND CLARK 1930:240 (range); BARNHART 1936:34 (description); HERALD 1940:64 (in part; diagnosed in key); 1941:62 (description; range; synonymy); MILLER AND LEA 1972:89 (description; range).

Siphostoma californiense; JORDAN AND GILBERT 1881:453 (synonymy); JORDAN AND JOUY 1881:1 (Santa Barbara, Monterey, and San Francisco); JORDAN AND GILBERT 1882:69 (in part; *S. griseolineatus* included); SWAIN 1882:308 (description; synonymy); JORDAN AND GILBERT 1883:384 (description; synonymy; range); SWAIN AND MEEK 1884:238 (diagnosed in key); JORDAN AND EVERMANN 1896:764 (description; synonymy; range).

Siphostoma californiensis; EVERMANN AND LATIMER 1910:136 (San Pablo Bay, California, probably *S. leptorhynchus*).

DIAGNOSIS.—A *Syngnathus* with 40–48 (42–46) dorsal rays; 12–14 pectoral rays; 3 anal rays; 19–22 (21) trunk rings; 46–52 (48–49) tail rings; 66–71 total rings; dorsal on 0.2–1.9 + 7.5–9.5 rings; total rings covered by dorsal 8.5–10.5; 19.5–25 rings covered by brood pouch; head 6.2–8.9 in SL; dorsal fin base 0.9–1.2 in head; snout 1.5–2.0 in head; maximum known size 533 mm SL; smallest mature male 191 mm SL. See Tables 4 and 5 for additional counts and measurements.

DESCRIPTION.—All ridges on body distinct, smooth, and rounded. Supraoccipital, nuchal, and prenuchal ridges absent. Opercular ridge reduced to absent. Snout ridge low, not elevated, and smooth, extending posteriorly to interorbit. Supraorbital ridge absent. Pectoral cover-plate ridges absent. Superior trunk ridge indistinct anterior to pectoral fin. Lateral trunk ridge and superior tail ridge overlap on first tail ring. Scutella small, about one-third depth of adjoining plates. Lateral line consisting of 7–8 papillae per plate. No dermal flaps.

Protecting plates of brood pouch well developed, about as high as half adjacent tail; margin of brood pouch folds smooth. Eggs 1.1–1.3 in greatest diameter, arranged in 2 layers 3–4 across. Males with young or eggs have been collected in July–October.

The fins are normally developed. Pectoral fin reaching posteriorly just past junction of first and second trunk rings. Caudal fin as long as last three tail rings.

Coloration in life. From C. L. Hubbs's field notes for SIO H45-69.

Belly generally yellow-green, sometimes pale blue or even pale brownish. Especially conspicuous are the small dark speckles, occasionally weak or absent, along the carinae of the trunk between the plates. These provide an almost invariable distinction. The streak along the mid-line of the belly is lacking or very weakly developed. In almost all

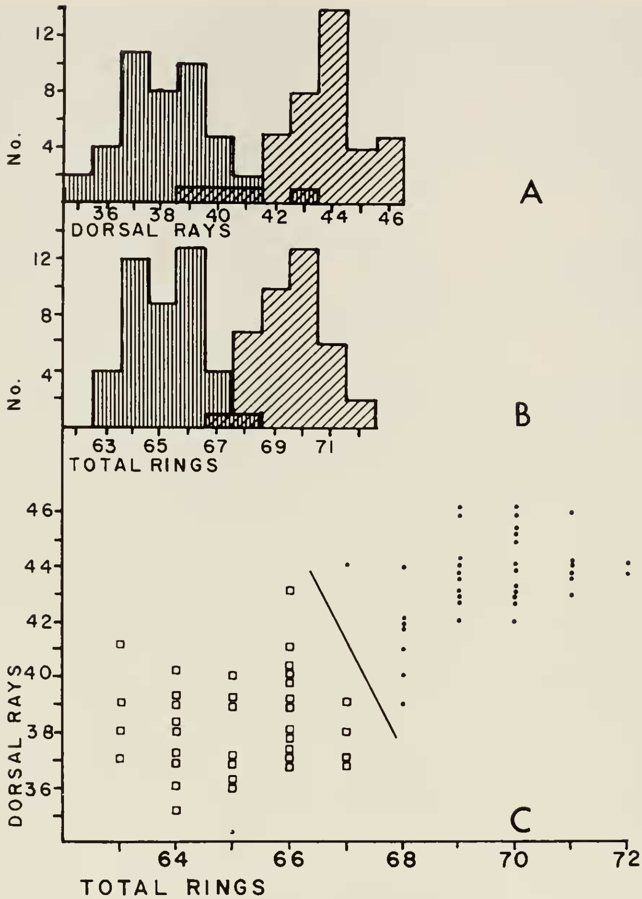

FIGURE 11. Comparison of meristic characters between *Syngnathus exilis* and *Syngnathus californiensis*. (*A*) Frequency of dorsal ray counts. *S. exilis* vertical lines, *S. californiensis* diagonal lines. (*B*) Frequency of total ring number. *S. exilis* vertical lines, *S. californiensis* diagonal lines. (*C*) Number of dorsal rays plotted against total number of rings. *S. exilis* open squares, *S. californiensis* dots.

specimens the light streakings in the upper and lateral aspects of the head and body form more or less definite and extensive wavy lengthwise lines, typically forming a ring on the first nuchal plate. When light markings are developed along the ventral carina of trunk (in about one-third of specimens) there tend to be more definite elliptical or oval marks more or less separated from the light color of the belly, and when they are developed similar marks are usually evident along the median and dorsal carinae.

Coloration in alcohol. The young, which are associated with drifting kelp, often are light gray to tan with a dark streak alongside the snout.

Adults vary from tan to brown, often with indistinct darker blotches and wavy lines about the head and opercle; especially pronounced along the sides of the trunk. The dark snout stripe most often remains as a dark area around and below the nostrils. The caudal has the same color as the body. The remaining fins are colorless except for melanophores along the rays.

HABITAT.—Offshore kelp (*Macrocystis*) beds, and frequently associated with drifting kelp.

COMPARISONS.—*S. californiensis* is a very distinctive fish as an adult. The combination of large size and high number of rings and dorsal rays serves to distinguish *S. californiensis* from all other California pipefishes. *S. euchrous* most closely approaches *S. californiensis* in size and number of rings, but its short round snout easily distinguishes it from the longer compressed snout of *S. californiensis*. *S. californiensis* juveniles are easily confused with adults of *S. exilis* (see comparison in account of *S. exilis*).

RANGE.—Bodega Bay, California, south to Bahía Santa María, Baja California, and including the offshore islands (essentially the same distribution as that of the giant kelps *Macrocystis pyrifera* and *M. angustifolia*).

MATERIAL EXAMINED.—**California:** Bodega Bay, CAS 32933, 1(162). San Francisco, CAS 60233, 2(154–171); USNM 27199, 1(401). Moss Landing, SIO 62-510, 1(284); SIO 53-194, 3(131–192). Monterey Bay, SU 19261, 1(128); SU 36465, 6(94–325); SU 5327, 3(157–184); CAS 13409, 1(177); SU 58461, 3(57–84). Guide Sea Mount, CAS 32983, 1(98). 36°N, 123°W, LACM 30458-1, 1(212). W. R. Hearst State Park, SIO 73-301, 13(174–254). Morro Bay, UCLA W50-196, 2(162–185). Diablo Cove, LACM 31300-24, 2(160–203). Avila Bay, SIO H50-195. Santa Barbara, SIO 61-426, 30(119–362); SIO H44-12, 1(173); SIO H51-128, 3(119–327). Santa Rosa Island, UCLA W50-99, 2(161–171). Santa Cruz Island, UCLA W50-87, 1(247); UCLA W50-97, 1(183). San Pedro, SIO H44-38. Long Beach, CAS 31512, 1(241). Del Mar, SIO 58-107, 2(400–410). Catalina Basin, S. Imsand personal collection, 16(78–100). La Jolla, SIO H52-181, 1(115); SIO H50-7, 1(437); SIO H47-153, 1(172). Bird Rock, SIO 75-427, 1(533). Mission Beach, SIO 67-29, 1(530). Mission Bay, SIO H45-8, 5(121–184); CAS 11428, 1(122); SIO H44-28, 1(125); SIO H46-75, 2(168–180). Point Loma, SIO H51-347, 7(151–387).

Mexico: Bahía de Todos Santos, SIO H53-229, 2(223–269); SIO 61-284, 13(111–323); SIO 64-806, 5(125–349). Punta Banda, SIO 59-302, 1(194). Cabo Colnett, SIO H50-62, 1(222). Isla San Martín, SIO H52-219, 1(89); SIO H52-218, 3(104–162). Bahía San Quintín, SIO H51-108, 1(141). Punta Baja, SIO H51-401, 1(198). Isla San Geronimo, SIO H52-159, 2(190–252). Bahía San Carlos, SIO H52-210, 16(175–282). Punta Eugenia, SIO H52-118, 1(125). Isla Cedros, CAS 32952, 1(224). Bahía Thurloe, CAS 15424, 1. Bahía Santa María, LACM W51-264, 1(234).

Syngnathus macrobrachium n.sp.

(Figure 10*A*)

Syngnathus acicularis (not of Jenyns); DELFIN 1901:42 (range); HILDEBRAND 1946:155 (in part; description; synonymy; range); MANN 1954:190 (description; range); KOEPCKE 1962:200 (range); DEBUEN 1963:91 (synonymy; description); MORROW 1957:228 (Peru); CLEMENS AND NOWELL 1963:262 (night light off Peru); CHIRICHIGNO-F. 1974:189, 351 (diagnosed in key; range).

Siphostoma aciculare (not of Jenyns); EVERMANN AND RADCLIFFE 1917:53 (synonymy; description); NICHOLS AND MURPHY 1922:506 (Chincha Island).

Syngnathus acus (in part, not of Linnaeus); HERALD 1940:60 (diagnosed in key); FOWLER 1944:496 (range).

DIAGNOSIS.—A *Syngnathus* with 36–44 (39–42) dorsal rays; 12–15 pectoral rays; 2–4 anal rays; 16–18 (17–18) trunk rings; 40–43 (41–42) tail rings; 57–62 total rings; dorsal on 0.5–2.3 + 7–9 rings; total rings covered by dorsal fin 9–10.3; 17–21 pouch rings; head 6.6–8.2 in SL; dorsal fin base 0.9–1.2 in head; snout 1.8–2.0 in head; maximum known size 255 mm SL; smallest mature male 84 mm SL. See Tables 4 and 5 for additional counts and measurements.

DESCRIPTION.—All ridges of body rounded and smooth. Nuchal and prenuchal ridges low, smooth. Opercular ridge extending posteriorly about one-fourth length of opercle. Supraorbital and snout ridges low, smooth. Ridges of pectoral cover plate obsolete. Trunk and tail ridges smooth, without indentations between rings. Superior trunk ridge does not extend anteriorly past gill opening. Scutella moderately developed, about equal in depth to adjacent plate. Lateral line consisting of 4–5 papillae per plate. No dermal flaps.

Protecting plates of brood pouch about as high as adjacent tail; margin of brood pouch folds smooth. Egg size unknown. Males with embryos and with recently emptied pouches have been taken from October through April.

The fins are well developed. The pectoral is particularly large, extending posteriorly over two full rings.

Coloration in alcohol. Generally a light brown to dusky with caudal fin darker. A dark streak on mid-ventral snout, another just anterior to orbit. Dorsal and pectoral fins colorless, with chromatophores present along sides of individual rays.

MERISTIC VARIATION.—There is little variation in the number of trunk rings. There is some indication that the Chilean population is characterized by having 18 trunk rings and the Peruvian by 17.

There is a greater variation in the number of tail rings. The range for Peruvian fish is usually 40–42, whereas the counts of the Chilean fish are fairly stable at 42.

The increase in number of rings with higher latitudes is not found in the count of dorsal rays. The Peruvian fish have 40–42 dorsal rays, whereas those from Chile have 39–40, if the fish from Hornitos and Valparaíso, Chile, are exluded.

COMPARISONS.—*S. macrobrachium* is very close to *S. carinatus* and *S. folletti* of the western Atlantic. It differs from *S. carinatus* in having a longer snout (1.6–1.8 rather than 1.8–2.0 in head), coloration dark rather than lighter gray, and a longer pectoral fin (extending posteriorly over two full rings rather than one to one and one-half). It differs from *S. folletti* in having longer pectoral fins, 36–44 dorsal rays rather than 37–38, and in having a longer head (6.6–8.2 in SL rather than 8.2–9.9).

RANGE.—Tumbes, Peru, south to Puerto Montt, Chile.

ETYMOLOGY.—From the Greek *makros*—long, and *brachion*—arm, in reference to the long pectoral fin.

MATERIAL EXAMINED.—**Holotype:** USNM 176501, 1(225), a mature male collected at Huasco, Chile (28°28'S, 71°14'W), on 9–10 Oct. 1844, by M. J. Lobell.

Paratypes: UCLA W59-49, 1(153), night light off Punta Berejo, Peru (10°34'S, 77°56'W), 16 Sep. 1959, by J. Seapin. SIO 72-168, 2(177–190), off Hornitos, Chile, 5 m, otter trawl, 27 Apr. 1972, by local fishermen aboard the Luz III. USNM 213485, 4(193–255), collected with holotype. UCLA W58-116, 3(92–103), bait net off Ilo, Peru (17°38'S, 71°18'W), 15 Dec. 1957, by J. Seapin. IMARPE uncat., 2(122–186), Zona de Lima, Peru, July 1973, by K. Freyman. IMARPE uncat., 10(123–161), Cantolao la Punta, Peru, 27 Apr. 1964, by B. M. Vildoso. EBMCh 10108–10109, 2(96–111), Iquique, Chile, Dec. 1957.

ADDITIONAL MATERIAL: **Peru:** Cabo Blanco, UCLA W59-46, 3(52–60). Callao, UCLA W59-48, 7(74–89). Lima, CAS 45073, 4(116–176). Bahía Chilca, USNM 127856, 3(89–175); USNM 127855, 1(107).

Chile: Valparaíso, CAS 12017, 1(126).

Syngnathus euchrous n.sp.

Syngnathus californiensis californiensis (in part, not of Storer); HERALD 1940:64; 1941:62.

DIAGNOSIS.—A *Syngnathus* with 33–45 dorsal rays; 11–14 pectoral rays; 3 anal rays; 18–20 trunk rings; 41–49 tail rings; 60–68 total rings; dorsal on 0.2–1.5 + 6–9 rings; brood pouch covering 20–23 rings; head 8.3–11.2 in SL; dorsal fin base 0.8–1.3 in head; snout 1.8–2.5 in head.

DESCRIPTION.—All ridges of body smooth to slightly rugose. Nuchal and prenuchal ridges low to obsolete. Opercle strongly convex, with weak ridge restricted to anterior fourth of opercle. Snout ridge development different in the two subspecies. Supraorbital ridge reduced. Interorbital flat to slightly concave. Pectoral cover plate with superior ridge obsolete to absent. Lateral trunk ridge ending on last trunk or first tail ring. Lateral line papillae 5–8 per plate. No dermal flaps.

Protecting plates of brood pouch varying from about one-third as high to about as high as adjacent tail. Eggs 1.2 mm in greatest diameter, arranged in 2–4 layers 4–6 across. Males with eggs and young collected from February through August.

COMPARISONS.—*S. euchrous* is most closely related to *S. leptorhynchus* from which it can be distinguished by the characters given in the key.

ETYMOLOGY.—From the Greek *eu*—well, and *chroa*—the color of the skin, in reference to the well-marked coloration.

Key to the Subspecies of
Syngnathus euchrous

1a. Dorsal rays usually 39–42; tail rings usually 45–46; 21–23 rings covered by brood pouch .... *euchrous*
Redondo Beach, California to Punta Eugenia, Baja California

1b. Dorsal rays usually 36–38; tail rings usually 42–44; 20–21 rings covered by brood pouch. .... *ollotropis* n.subsp.
Bahía Tortugas to Bahía de Ballenas, Baja California

Syngnathus euchrous euchrous

(Figure 12*A*)

DIAGNOSIS.—An *S. euchrous* with 38–45 (39–42) dorsal rays; 11–14 pectoral rays; 3 anal rays; 18–20 (19) trunk rings; 42–49 (45–46) tail rings; 61–68 total rings; snout ridge concave in outline, smooth; maximum known size 296 mm SL; smallest sexually mature male 128 mm SL. See Tables 4, 5, and 6 for additional counts and measurements.

Coloration in life. From C. L. Hubbs's field notes for SIO H47-43:

> Four are rich brown, grading from greenish brown to reddish brown with very conspicuous pearly cross-blotching. There are a variable number of blue-white specks. The crown and nape regions are more or less completely covered with fine to coarse speckles. Along the ventrolateral keel there are single to compound specks on the plates . . . . The opercles are flecked with silver-blue and a more or less distinct wedge of the same color extends downward and backward from eye. The dorsal fin is entirely or almost entirely immaculate.

Coloration in alcohol. As is true with most species of *Syngnathus*, excessive variability precludes using color patterns as diagnostic features. A dusky patch or streak below the nares. A series of small whitish spots over the entire dorsal surface of head and body, often extending onto sides. Protecting plates of brood pouch chocolate-brown. Caudal brownish with white on tips of outermost rays. Dorsal and pectoral fins translucent, with some pigmentation along rays.

HABITAT.—Near bottom off rocky shores.

RANGE.—Redondo Beach, California, south to Punta Eugenia, Baja California.

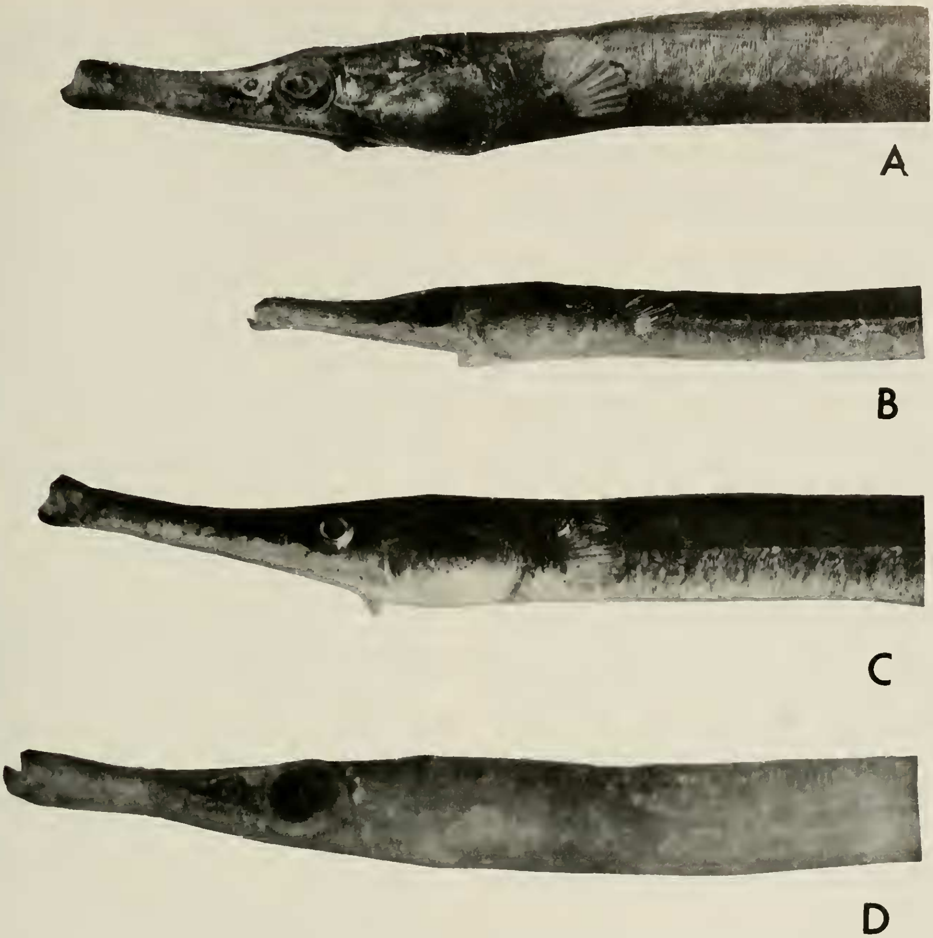

FIGURE 12. Anterior part of body of four species of eastern Pacific Syngnathidae. (*A*) *Syngnathus euchrous*, holotype, SIO H47-68. (*B*) *Syngnathus euchrous ollotropis*, holotype, SIO H48-53. (*C*) *Syngnathus leptorhynchus*, a 166-mm-SL male, SIO 63-1053. (*D*) *Syngnathus insulae*, holotype, SIO 63-169.

MATERIAL EXAMINED.—**Holotype:** SIO H47-68, a 232-mm-SL mature male collected at Bahía Todos Santos, Baja California (31°52′N, 116°38′W), with a 25-ft (7.6-m) beach seine at a depth of 0.3–1.5 m on 22 May 1947, by Carl L. and Laura C. Hubbs.

Paratypes: SIO H47-68, 86(83–228), same data as holotype. SIO H48-319, 16(95–204), E side of southern Isla Coronado, Baja California, dredge, 11 m, 22 Dec. 1948, by Clark Hubbs and party aboard M/V ORCA. GCRL 15757, 22(96–175), Scripps Pier, La Jolla, California, dip net under night light, 17 Aug. 1947, by J. L. McHugh. CAS 27405, 11(39–186), Estero de Punta Banda, Baja California, 8 Sep. 1949, by Chaffy, Scott, and Mead.

ADDITIONAL MATERIAL.—**California:** Redondo Pier, SIO H48-204, 1(225). Scripps Pier, SIO H46-63, 20(54–179). La Jolla Shores, SIO H50-214, 2(175–249); SIO H50-227, 5(119–139).

Baja California: Islas Coronados, SIO H49-217, 17(142–224); SIO H49-19, 15(152–223); SIO H46-125, 4(86–118); SIO H46-119, 11(132–222); SIO H48-217, 14(107–238). Bahía de Todos Santos, SIO H45-223a, 4(111–213); SIO H51-48, 5(99–130). Bahía Blanca, SIO 60-327, 5(162–203). Isla Cedros, SIO 53-110, 6(123–186); SIO 68-280, 1(113).

INTERGRADES with *S. e. ollotropis*: Punta Malarrimo, UCLA W51-223, 6(61–223); UCLA W51-221, 12(76–149).

Syngnathus euchrous ollotropis n.subsp.

(Figure 12*B*)

DIAGNOSIS.—An *S. euchrous* with 33–40 (36–38) dorsal rays; 11–13 pectoral rays; 3 anal rays; 18–20 (19) trunk rings; 41–45 (43) tail rings; 60–65 total rings; snout ridge well developed from vomer to anterior third of orbit, rugose, typically without distinct rise anterior to orbit; maximum known size 224 mm SL; smallest sexually mature male 102 mm SL. See Tables 5 and 6 for additional counts and measurements.

Description.—Young. 14–16 mm SL at birth. All fins developed and with rays. Rings without prominent spines but distinct triangular ridges. Uniform orange-tan with middle rays of caudal fin more darkly pigmented than outer. Dorsal and pectoral fins colorless. Anal fin darkly pigmented.

Coloration in life. From C. L. Hubbs's field notes for SIO H48-53:

> The lower part of opercles dark and mottled . . . . Streaked color phase frequent and light bars usually faint and seldom well developed . . . the lower parts are almost always marked with dark and usually variegated rather than being clear. In general the color pattern is more longitudinal and less transverse. In some specimens the lower keel carries a series of light blotches one per segment or may be largely clear. The general color varies from light tan to very deep purple-brown, almost black. The prominent marking of the lower surface is perhaps the most outstanding color feature.

Coloration in alcohol. Typically brownish above and light below, becoming entirely brownish on posterior third of body. Dorsal fin hyaline. Anal and pectoral rays bordered by melanophores. Often a dark midventral stripe on trunk. A chocolate-brown band on trunk between lateral trunk ridge and superior tail ridge. Caudal with light and dark reticulations. A reticulated area around orbit and on snout. Most often an orange-brown body with longitudinal lighter streaks.

Habitat.—Eelgrass beds and drifting algae.

Comparisons.—*S. e. euchrous* is easily distinguishable from *S. e. ollotropis* by the characters given in the key. There is, however, a zone of intergradation along the coast near Punta Malarrimo. The specimens examined from there are intermediate in meristic characters between the two subspecies (Table 6). Although these intergrades are closer to *S. e. euchrous* in the ranges of these meristic characters, they have the distinctive straight snout ridge characteristic of *S. e. ollotropis*.

The semi-isolation of *S. e. ollotropis* in Turtle Bay has produced a distinctive morphology which would have to be considered specifically distinct had not the intergrades been collected.

The existence of definite intergrades between *S. e. euchrous* and *S. e. ollotropis* is concrete indication that subspecific recognition is warranted.

Range.—Bahía Tortugas south to Bahía de Ballenas, and Isla Cedros, Baja California.

Material Examined.—**Holotype:** SIO H48-53, a 224-mm-SL mature male collected ¾ mile [1.2 km] E of Cabo Tortolo, Bahía Tortugas, Baja California (27°38′53″N, 114°51′46″W), from eelgrass at a depth of 1 m, with an 8-ft [2.4-m] minnow seine, 8 Feb. 1948, by Clark and Earl L. Hubbs.

Paratypes: All collected in Baja California. SIO H48-53, 35(43–220), same data as holotype. SIO H48-55, 47(66–216), same locality as holotype, 1.5 m, 25-ft [7.6-m] bag seine, 9 Feb. 1948, by Clark and Earl Hubbs. GCRL 15758, 15(61–158), same locality, 1 m, 25-ft [7.6 m] bag seine, 7 Feb. 1948, by Clark and Earl Hubbs. SIO H47-112, 1(207), Bahía Tortugas, from drifting brown algae, 23 May 1947, by Robert S. Arthur. SIO 54-131, 1(139), SE part of Bahía Tortugas, shell dredge, R/V Orca, 18 July 1954, by J. W. Sefton, Jr. SU 19260, 1(144), off Isla Cedros, 27 Mar. 1952, by James E. Böhlke and party, Sefton-Stanford Orca Expedition.

Additional Material.—Bahía Tortugas, CAS 5438-5440, 3(104–112). Bahía de Ballenas, SIO 64-847, 1(135).

Syngnathus leptorhynchus Girard

(Figures 12*C*, 13, 14)

Syngnathus brevirostris Girard, 1854:156 (original description; San Diego, California; cotypes USNM 969; nec *S. brevirostris* Rüppell, 1840).

Syngnathus leptorhynchus Girard, 1854 (Oct. 6):156 (original description; San Diego, California; holotype USNM 970, lost); Jordan and Evermann 1896:764 (description; range; synonymy); Jordan and Gilbert 1880:23 (synonymy); Starks and Morris 1907:184 (habits; range); Hubbs 1916:158 (description); 1921:1 (synonymy; description); Ulrey and Greeley 1928:42 (synonymy; range); Ulrey 1929:6 (listed); Jordan, Evermann, and Clark 1930:240 (synonymy; range); Barnhart 1936:34 (description); Miller and Lea 1972:87 (description; range).

Syngnathus californiensis leptorhynchus; Herald 1940:64 (new combination; diagnosed in key); 1941:66 (description; range; synonymy).

Siphostoma leptorhynchus; Jordan and Gilbert 1881:453 (synonymy); Jordan and Jouy 1881:1 (*S. dimidiatus* as synonym); Jordan and Gilbert 1882:69 (range); Swain and Meek 1884:238 (key); Jordan and Gilbert 1883:384 (description; range; synonymy).

Siphostoma leptorhynchum; Swain 1882:311 (synonymy; description).

Syngnathus griseolineatus Ayres, 1854 (Oct. 27):14 (original description; probably near San Francisco, California; holotype ANSP 835); Starks 1911:177 (breeding habits); Hubbs 1916:159 (measurements; compared with *S. barbarae*); 1921:1 (counts and measurements); Jordan, Evermann, and Clark 1930:240 (range).

Syngnathus californiensis griseolineatus; Herald 1940:64 (diagnosed in key); 1941:65 (description; range; synonymy).

Siphostoma griseolineatum; Swain 1882:308, 310, 315 (key; synonymy; description); Swain and Meek 1884:238 (key); Kermode 1909:83 (British Columbia); Evermann and Latimer 1910:136 (Tomales Bay, California); Kermode 1929:24 (Victoria, British Columbia); 1930:22 (Longborough Inlet, British Columbia); Jordan and Evermann 1896:764 (description; range; synonymy).

Syngnathus abbotti GIRARD, 1859:346 (original description; San Francisco, California; holotype USNM 971).
Syngnathus arundinaceus GIRARD, 1859:346 (original description; coast of California; holotype USNM 972); JORDAN, EVERMANN, AND CLARK, 1930:240 (range).
Syngnathus dimidiatus GILL, 1863:284 (replacement name for *Syngnathus brevirostris* Girard, preoccupied).
Siphostoma bairdianum (not of Duméril) SWAIN, 1882:311 (description; Santa Barbara, California).
Siphostoma barbarae SWAIN *in* SWAIN AND MEEK, 1884:238 (based on specimen described by Swain (1882) as *S. bairdianum*; holotype USNM 31253); JORDAN AND EVERMANN 1896:765 (description; synonymy; range).
Syngnathus barbarae: STARKS AND MORRIS 1907:185 (Santa Barbara); HUBBS 1916:159 (description); ULREY AND GREELEY 1928:42 (synonymy; range); JORDAN, EVERMANN, AND CLARK 1930:240 (range).
Syngnathus californiensis (in part, not of Storer): FOWLER 1921:443 (description); STARKS 1911:177 (Puget Sound).

DIAGNOSIS.—A *Syngnathus* with 28–43 dorsal rays; 11–13 pectoral rays; 2–3 anal rays; 16–21 trunk rings; 36–46 tail rings; 53–63 total rings; dorsal on 0–1.5 + 6–9 rings; brood pouch covering 18–26 rings; head 5.6–9.3 in SL; dorsal fin base 0.9–1.3 in head; snout 1.6–2.4 in head; maximum known size 299 mm SL; smallest mature male 80 mm SL. See Tables 4, 5, 7, and 8 for additional counts and measurements.

DESCRIPTION.—All ridges of head and body moderately developed, rounded, and rather smooth to slightly rugose. Nuchal and prenuchal ridges low. Supraoccipital ridge obsolete and not continuous with nuchal ridge. Opercular ridge extends posteriorly about one-third length of opercle. Snout ridge smooth, low, with small hump over nares. Superior ridge of pectoral cover plate smooth, curved; inferior ridge obsolescent to absent. Supraorbital ridges smooth. Northern populations tend to have more obsolescent ridges. Trunk and tail ridges slightly rugose. Superior tail and lateral trunk ridges usually not overlapping; when overlapping, only for length of last trunk ring. Scutella of medium size, subequal to half depth of adjoining plates. Lateral line consisting of 6–9 papillae per plate. No dermal flaps.

Protecting plates of brood pouch moderately developed and as much as two-thirds as deep as attached tail ring; edges of brood pouch folds entire. Eggs 1.3–1.5 mm in greatest diameter, arranged in 1–2 layers 4 across. Males with eggs and young collected year round.

Fins moderately developed. Caudal as long as last three tail rings. Pectoral fin extends posteriorly over about 1⅓ rings.

TABLE 6. MERISTIC VARIATION IN *Syngnathus euchrous*.

Subspecies and locality	Trunk rings			Tail rings									Dorsal rays												
	18	19	20	41	42	43	44	45	46	47	48	49	33	34	35	36	37	38	39	40	41	42	43	44	45
S. e. euchrous																									
La Jolla	9	16	2	—	1	—	1	2	13	7	1	2	—	—	—	—	—	—	1	2	3	5	3	6	2
Coronados Is.	—	14	11	—	—	—	—	7	9	3	3	—	—	—	—	—	—	3	10	8	—	2	1	—	2
Todos Santos	8	7*	4	—	—	1	2	6	8	1*	1	—	—	—	—	—	—	2	5	4	2	3*	2	—	—
Blanca Bay	3	2	—	—	—	—	—	2	2	1	—	—	—	—	—	—	—	1	—	—	2	—	2	—	—
Cedros Island	4	4	—	—	—	—	4	3	—	—	1	—	—	—	—	—	—	—	—	2	—	4	1	—	1
Intergrades																									
Puerto Malarrimo	5	6	—	—	1	3	3	3	1	—	—	—	—	—	—	—	2	2	2	—	4	—	—	—	—
S. e. ollotropis																									
Turtle Bay	10	84**	8	5	25	40	27**	3	—	—	—	—	1	9	10	24	22**	21	12	2	—	—	—	—	—

* Holotype of *S. e. euchrous*.
** Holotype of *S. e. ollotropis*.

TABLE 7. MERISTIC VARIATION IN *Syngnathus leptorhynchus*.

	Trunk rings						Tail rings										
Locality	16	17	18	19	20	21	36	37	38	39	40	41	42	43	44	45	46
Vancouver Is.	—	—	11	17	—	—	—	—	—	—	3	8	8	4	2	—	—
Puget Sound	—	5	21	4	—	—	—	—	—	—	2	10	12	7	—	—	—
Coos Bay	—	1	51	9	1	—	—	—	—	—	—	4	12	14	27	3	—
Humboldt Bay	—	3	64	19	1	—	—	—	—	—	—	4	28	28	21	6	—
Tomales Bay	—	2	31	4	—	—	—	—	—	—	7	11	16	3	—	—	—
San Francisco Bay	—	2	10	190*	52	1	—	—	—	—	—	3	32*	109	107	20	1
Morro Bay	—	1	35	3	1	—	1	1	10	15	10	3	—	—	—	—	—
Pt. Mugu Lagoon	—	—	14	—	—	—	—	—	1	4	6	3	—	—	—	—	—
Santa Barbara	—	—	1†	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Newport Bay	—	2	17	11	—	—	—	—	1	2	7	5	11	3	—	—	—
Mission Bay	3	91	144	9	—	—	4	19	61	74	64	21	3	—	—	—	—
San Diego Bay	1	14**	9**	1	—	—	—	2	12	9**	2	—	—	—	—	—	—
Estero de Punta Banda	2	12	5	—	—	—	—	4	8	4	—	1	1	—	—	—	—
Bahía San Quintín	—	10	29	—	—	—	6	14	15	3	1	—	—	—	—	—	—
Scammon Lagoon	3	3	1	—	—	—	—	1	1	1	2	2	—	—	—	—	—
Total	9	146	443	267	55	1	11	41	109	112	104	75	123	168	157	29	1
			$\bar{x} = 18.2 \pm 0.8$									$\bar{x} = 41.2 \pm 2.3$					

	Dorsal rays															
Locality	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
Vancouver Is.	—	—	—	—	—	—	2	1	6	4	7	3	1	1	1	—
Puget Sound	—	—	—	—	—	—	2	3	8	7	4	2	2	—	—	—
Coos Bay	—	—	—	—	—	—	—	—	5	4	16	14	10	8	2	—
Humboldt Bay	—	—	—	—	—	—	—	—	7	9	12	17	14	12	8	2
Tomales Bay	—	—	—	—	—	—	—	1	4	9	11	3	4	1	2	—
San Francisco Bay	—	—	—	—	—	—	1	9	31	55	61*	60	25	8	1	—
Morro Bay	—	—	—	—	3	5	10	10	6	5	—	—	—	—	—	—
Pt. Mugu Lagoon	—	—	—	—	2	2	2	5	2	1	—	—	—	—	—	—
Santa Barbara	—	—	—	—	—	—	—	—	1†	—	—	—	—	—	—	—
Newport Bay	—	—	—	—	3	5	6	6	7	3	1	—	—	—	—	—
Mission Bay	2	15	26	38	53	51	37	18	6	1	—	—	—	—	—	—
San Diego Bay	—	—	5	3	8	6	2	1**	—	—	—	—	—	—	—	—
Estero de Punta Banda	2	2	7	5	3	—	—	—	—	—	—	—	—	—	—	—
Bahía San Quintín	—	—	—	4	14	7	8	3	2	—	1	—	—	—	—	—
Scammon Lagoon	—	1	1	—	1	—	3	1	—	—	—	—	—	—	—	—
Total	4	18	39	50	87	76	73	58	85	98	113	99	56	30	14	2
								$\bar{x} = 35.8 \pm 3.3$								

* Holotype of *S. barbarae*.
† Holotype of *S. abbotti*.
** Syntypes of *S. brevirostris*.

Coloration in life. Mostly browns, purples, and greens, with varying amounts of mottling, spots, etc.

Coloration in alcohol. Coloration highly variable, mainly shades of brown. Great inter- and intra-population variability. Highly mottled, blotched, and striped. Dorsal fin always with some brownish spots at base and fin rays bordered with melanophores.

HABITAT.—Ordinarily inhabiting eelgrass in bays and occasionally near shore outside.

VARIATION AND GROWTH.—Variation: *Syngnathus leptorhynchus* shows extreme variation in meristic characters (see Table 7) approaching the North Atlantic species *S. typhle* in this regard. Duncker (1908) statistically analyzed several meristic characters of *S. typhle* populations from the Baltic Sea, Plymouth, and Naples and showed a definite clinal pattern in the variation of numbers of trunk rings and pectoral rays. Other meristic features showed populational differences, but in a mosaic pattern of different sequences.

Meristic variation in *S. leptorhynchus* is mosaic, and no single character allows or justifies recognition of more than one species or subspecies. Herald (1940, 1941) and others have used the same meristic characters herein analyzed in support of recognizing northern and southern species or subspecies. A mosaic pattern of variation is not limited to *Syngnathus* species, e.g., Rosenblatt (1963) reported a similar pattern for populations of the Central American tripterygiid *Enneanectes sexmaculatus*.

Each bay along the west coast of North America appears, on the basis of available evidence, to support a distinctive population of *S. leptorhynchus*. Meristic features of each population are not stable, but do fluctuate with changes in environmental temperature.

To underscore this point, C. L. Hubbs analyzed three collections from the northwest corner of Mission Bay on 22–24 April 1923. All three collections were made with exactly the same method (seine) and at the same location in the bay. For analysis, all specimens 97 mm SL or less are considered to be winter reared, and in view of the demonstrated growth (see below) it may be presumed that all specimens longer than 97 mm SL were at least mostly reared in warmer water. The summary of meristic data (Table 8) compiled for these collections indicates that the winter-reared young have higher means in all meristic characters studied than do the larger (adult) fish. The means for these two size groups are all significantly different ($P \ll .005$).

Although Mission Bay has been highly modified in recent years, the data are indicative of changes in meristic characters as a result of environmental temperature. Similar seasonal meristic variation has been documented by Brothers (1975) for the goby *Quietula y-cauda*—using samples taken throughout the year, he determined that the mean vertebral number of the postlarvae is inversely correlated with seasonal changes in environmental temperature.

Each local population of *Syngnathus leptorhynchus* is therefore distinctive and also highly modified by local environmental conditions. *S.*

TABLE 8. SEASONAL VARIATION IN MERISTIC CHARACTERS OF *Syngnathus leptorhynchus*.

	Trunk rings							Tail rings										
	17	18	19	N	$\bar{x}$	SD	*t*	36	37	38	39	40	41	42	N	$\bar{x}$	SD	*t*
Young	25	84	8	117	17.8	0.51	10.75			10	34	52	18	3	117	39.7	0.91	10.15
Adults	54	53	1	111	17.5	0.57		3	15	42	36	11	3		110	38.4	1.02	

	Total rings												Dorsal rays												
	53	54	55	56	57	58	59	60	N	$\bar{x}$	SD	*t*	29	30	31	32	33	34	35	36	37	N	$\bar{x}$	SD	*t*
Young			2	13	41	39	18	4	117	57.6	1.04	10.75	2	4	8	24	29	27	16	6	1	117	33.2	1.55	7.80
Adults	3	10	31	36	16	11	3		110	55.9	1.29		8	20	25	25	21	10	2			111	31.6	1.47	

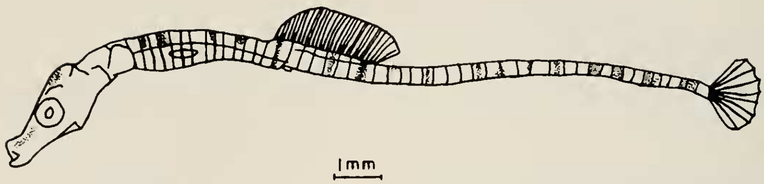

FIGURE 13. *Syngnathus leptorhynchus* at time of emergence from brood pouch. 16.3 mm SL.

leptorhynchus may be a useful indicator species for the effects of pollution.

Growth: On 16 June 1974, a male *S. leptorhynchus* (165 mm SL) gave birth to 85 young in the laboratory of the National Marine Fisheries Service, La Jolla. The young were immediately separated from their father and kept alive until a failure in the seawater system on 6 Sep. The young were fed *Artemia* nauplii and fresh-caught plankton. An overabundance of food was always present. Samples of the young were removed frequently during the period from 16 June to 6 Sep. and preserved in 10% formalin for later analysis.

Figure 14 represents the measured growth of the young for the period. The data have been analyzed and fitted to a Laird-Gompertz equation (Laird, Barton, and Tyler 1968) calculated after the methods of Zweifel and Lasker (1976). The Laird-Gompertz equation is preferred when analyzing growth for periods less than one year.

On 16 Aug. development of the brood pouch had already begun in a 76-mm-SL individual. Four males (80–93 mm SL), each with a fully developed brood pouch, were found on 24 Aug. By the termination of the experiment on 6 Sep., the largest specimen was a fully-mature, 114-mm male.

That the ranges of meristic variation for the adults do not completely subtend the ranges for the young together with rapid growth to sexual maturity strongly indicate that individuals of *S. leptorhynchus* (at least from Mission Bay) probably live for only one year. This is in agreement with the data presented by Brown (1972) for *S. louisianae*, *S. scovelli*, *S. floridae*, and *Micrognathus crinigerus* for Cedar Key, Florida. Based on length-frequency analyses, Brown estimated a life span of perhaps one year.

COMPARISONS.—A highly variable species that is similar to the Japanese *S. schlegeli*. In fact, it is rather difficult to separate members of northern populations of *leptorhynchus* from those of *schlegeli*. However, *S. schlegeli* has a longer snout and longer fins, and the ridges of the body are better developed. *S. insulae*, also closely related to *S. leptorhynchus*, may be distinguished by the characters given in the account of that species.

RANGE.—Southeastern Alaska south to Bahía Santa María, southern Baja California.

MATERIAL EXAMINED.—**Alaska:** UW 14486, 1(179); UW 1610, 1(212).

British Columbia: Vancouver, BC 53-253a, 28(60–206); SIO 62-206, 2(137–192).

Washington: Puget Sound, CAS 10935, 3(125–140); UW 4927, 3(136–151); UW 5296, 2(146–245); UW 4258, 3(86–130); UW 4918, 4(139–167); SIO 74-73, 19(73–215).

Oregon: Tillamook, UMMZ 93951, 33(49–235). Coos Bay, UMMZ 93956, 63(35–235).

California: Klamath Lagoon, CAS 45070, 1(216). Humboldt Bay, HSU OT62-7, 44(136–207); HSU OT61-18, 14(121–218); HSU OT64-5, 12(110–210). Mendocino County, SU 20515, 5(165–214). Tomales Bay, SIO 75-459, 37(54–234); UCLA W55-198, 35(61–207); CAS 19860, 2(211–293); CAS 26207, 2(104–252). Drakes Bay, CAS 7518, 1(130). San Pablo Bay, CAS 45072, 33(59–272). San Francisco Bay, SU 4190, 24(115–159); USNM 971, 1(228), holotype of *S. arundinaceus*; UMMZ 64416, 1(215); UMMZ 6044, 1(151); CAS ALBATROSS Biological Survey of San Francisco Bay*, D5826, 1(131); H5159, 2(139–165); D5816, 1(129); H5311, 1(119); H5013, 4(111–184); D5847, 1(92); H5003, 1(87–121); H5318, 2(110–128); H5185, 1(61); D5848, 2(101–118); H5312, 2(66–94); H5004, 2(77–110); H5308, 1(67); H5230, 1(62); H5248, 1(64); H5259, 1(61); H5310, 1(80); H5316, 2(69–98); H5309, 2(106–120); H5250, 7(51–123); H5009, 9(33–109); H5257, 1(86); H5261, 2(41–43); H5345, 13(25–133); H5313, 6(69–93); H5251, 6(73–125); H5010, 2(33–66); H5005, 3(44–69); H5275, 3(38–70); H5315, 5(63–113); H5252, 5(62–95); H5317, 4(76–103); H5311, 8(75–90); H5274, 8(67–77); H5007, 11(28–108); H5314, 13(67–105); H5272, 17(64–146); H5276, 25(49–130); H5006, 76(27–116). Elkhorn Slough, SIO 62-510, 3(77–103). Del Monte, SIO 48-372, 2(92–196). Morro Bay, SIO H50-191, 1(243); UCLA W50-196, 50(98–236); SU 48888, 10(162–217). Point Mugu, CAS 45076, from E. S. Herald personal collection, 4(151–181). Santa Barbara, USNM 31253, type of *S. barbarae*. San Pedro, SIO H48-180, 1(257). Newport Bay, UCLA W50-171, 50(99–278); UCLA W50-172, 3(101–132); SIO H46-33, 5(215–280). San Juan Capistrano, SIO H52-109, 1(101). Mission Bay, SIO H45-8, 50(72–198); SIO H46-10,

* Station data may be found in Anonymous 1921.

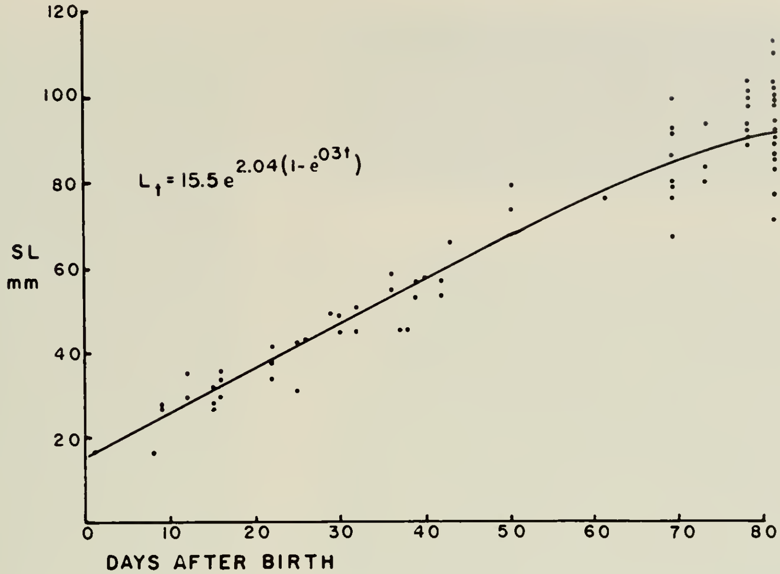

FIGURE 14. Growth of *Syngnathus leptorhynchus*. Standard length plotted against time in days. The Laird-Gompertz Equation fitted to these data is included.

3(116–125). San Diego Bay, USNM 969, 3, types of *S. brevirostris*; SIO 64-337, 25(100–158).

Baja California: Estero de Punta Banda, SIO H45-15, 19(104–158). Bahía San Quintín, SIO 60-453, 128(69–245); SIO 60-450, 6; SU 15251, 10(123–299). Laguna Scammon, SIO H52-140, 1(95). Bahía Santa María, SIO H50-149; SIO 60-294, 1(94).

Syngnathus insulae n.sp.
(Figure 12*D*)

DIAGNOSIS.—A *Syngnathus* with 31–34 (32–33) dorsal rays; 10–12 pectoral rays; 2–4 anal rays; 17–19 (18) trunk rings; 40–42 (41–42) tail rings; 58–60 total rings; dorsal on 0.2–1.2 + 6.5–8 rings; 19 rings covered by brood pouch; head 8.6–9.3 in SL; dorsal fin base 1.0 in head; snout 1.7–2.3 in head; maximum known size 204 mm SL; smallest sexually mature male 125 mm SL. See Tables 4 and 5 for additional measurements.

DESCRIPTION.—All ridges of head and body poorly developed, smooth. Prenuchal and nuchal crests obsolete. Opercular ridge reduced to short basal portion. Ridges of pectoral cover plate low. Trunk and tail ridges low, rounded but distinguishable. Superior tail ridge not reaching beyond first tail ring, only overlapping lateral trunk ridge for one-half ring. Scutella quite distinct and about half as deep as adjoining plate. Lateral line consisting of 5–6 papillae per plate. No dermal flaps.

Protecting plates of brood pouch well developed, each about as deep as adjacent tail ring; edges of brood pouch folds entire. Eggs 1.2–1.3 mm in greatest diameter, arranged in one layer two across. Males with eggs and young have been collected in April.

Fins normally developed. Caudal fin as long as last three tail rings. Pectoral fin reaches posteriorly to end of first trunk ring.

Young. About 12 mm SL at birth. About five dark bands posterior to vent. Body sprinkled with small round melanophores, especially in the area of the bands. Snout short, mouth distinctly upturned.

Coloration in life. From C. L. Hubbs's field notes for SIO H46-143:

> The greener specimen has a dark streak running downward and backward from eye. In this specimen the streak extending upward and backward from eye is less distinct. The streak running forward from eye to chin is conspicuous posteriorly but interrupted anteriorly. The redder specimen has a dark spot just behind and below eye, but no definite streaks radiating from eye.

Coloration in alcohol. A light tan to tan fish without any distinguishing pattern. The caudal fin may be lighter at its border. Darker specimens may have a sprinkling of small melanophores bordering rays.

HABITAT.—Occasionally in floating *Sargas-*

sum, but much more often taken at depths of 20–34 m in beds of *Sargassum* and algae.

COMPARISONS.—Appears most closely related to *S. leptorhynchus*. The two are very close in meristic characters. *S. leptorhynchus* has the longer snout and postorbital. *S. insulae* differs from *leptorhynchus* in the broader interorbital, smaller orbit, and less robust body.

RANGE.—Endemic to Isla Guadalupe, an oceanic island well off the coast of Baja California.

ETYMOLOGY.—From the Latin *insulae*, genitive of *insula* (island).

MATERIAL EXAMINED.—**Holotype:** SIO 63-169, a 160-mm-SL mature male collected at Caleta Malpómene, a cove at the south end of Isla Guadalupe, Mexico, from a depth of 22–50 m using a try-net on 22 Apr. 1963, by C. L. Hubbs and party aboard the R/V HORIZON.

Paratypes: All taken from Isla Guadalupe. SIO 63-169, 32(77–204), same data as holotype. SIO H46-143, 2(98–98.4), Caleta Melpómene, under nightlight, 6 Dec. 1946, by C. L. Hubbs aboard R/V E. W. SCRIPPS. SIO H46-144, 1(118), Caleta Melpómene, 3–6 m, dredge, 7 Dec. 1946, by C. L. Hubbs aboard R/V E. W. SCRIPPS. GCRL 15756, 2(93–117), Caleta Melpómene, under nightlight, 27 Jan. 1950, by C. L. Hubbs and party aboard R/V ORCA. SIO H50-31, 1(99), Caleta Melpómene, 3–7 m, dredge, 29 Jan. 1950, by C. L. Hubbs and party aboard R/V ORCA. SIO 54-214, 2(51–87), ⅛ mile [200 m] "off Barracks" (Northeast Anchorage), under nightlight, 13 Nov. 1964, by C. L. Hubbs and party. SIO 63-188, 1(116), just inside s side Punta Amarillo on rocky bottom, 15 m, Chemfish and SCUBA, 26 Apr. 1963, by J. R. Stewart and party.

FOSSIL SYNGNATHIDAE OF SOUTHERN CALIFORNIA

The following discussion of the fossil pipefishes of southern California is based on a large collection in the Section of Vertebrate Paleontology at the Natural History Museum of Los Angeles County (LACM), including the collections formerly housed at the California Institute of Technology (CIT).

The fossil syngnathids from southern California are all of Miocene to possibly Pliocene age. Most specimens have been collected in diatomites and diatomaceous siltstones of the upper Modelo and Puente formations, although a number have been collected from argillaceous diatomites of the lower Modelo Formation. Localities are given by number, and more precise data can be obtained by referring to the Locality Catalogue in the Vertebrate Paleontology Section (LACM).

These formations have provided the bulk of material used in the descriptions of California fossil fish (Jordan and Gilbert 1919; David 1943). Since most of the fishes contained in these deposits are pelagic to bathypelagic, previous authors have inferred that during the Miocene this area was a large basin with depths ranging from 200–500 m (David 1943) to 1000 m (Crane 1966).

Materials and Methods

The anal and pectoral fins of fossil pipefishes are usually not visible. Since the anal fin marks the first tail ring, it is impossible to make precise counts of trunk and tail rings. However, the number of plates in a ring around the trunk is usually seven and there are four around the tail. When these plates could be seen, accurate counts were made. When such counts were not determinable, the trunk rings were counted as ending at the first ring under the dorsal fin or the posterior end of the median ventral ridge (in *Hipposyngnathus*).

The count of dorsal fin rays in fossil pipefishes is difficult because of frequent splitting of the two ray-halves. However, with proper precaution, a fairly accurate count is often possible.

Accurate counts of the rings and dorsal rays are of particular importance in syngnathid taxonomy, as these counts provide the primary basis for classification of living forms.

Correct generic allotment of fossil syngnathid species is based primarily on the author's knowledge of the general appearance of syngnathid genera. The characters often used for placement of syngnathids into a genus (i.e., lateral ridge pattern, placement and position of brood pouch) are very rarely preserved in fossilized pipefishes.

This section on fossil pipefishes is intended only to describe those forms known to occur in deposits along the eastern Pacific and is not meant to be a critical review or stratigraphic analysis of them.

Subfamily **Hipposyngnathinae** nom. nov.

Eogastrophinae JERZMANSKA 1968:436 ("genre typique: *Hipposyngnathus* Danil'chenko 1960").

Since the subfamily name was incorrectly proposed as Eogastrophinae (the sole-included genus is *Hipposyngnathus*), and since subfamilial ranking is obviously called for, I propose the name Hipposyngnathinae, with *Hipposyngnathus* as the type-genus.

Jerzmanka diagnosed the subfamily adequate-

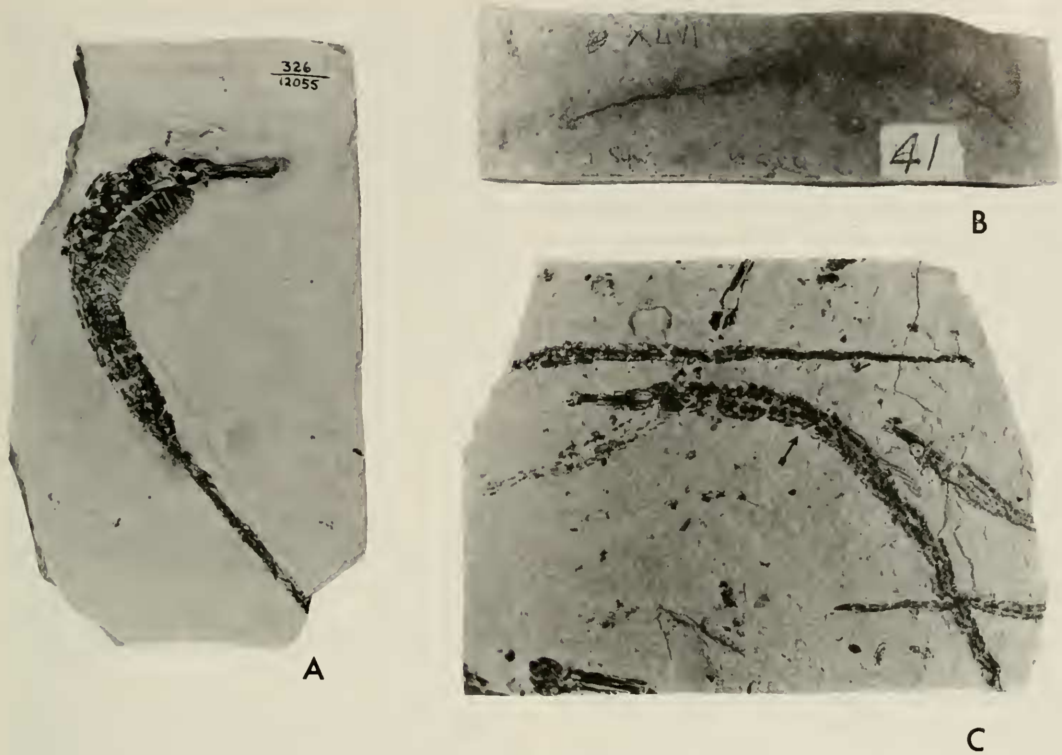

FIGURE 15. Holotypes of three species of California fossil syngnathids. (*A*) *Hipposyngnathus imporcitor*, LACM 12055. (*B*) *Syngnathus avus*, CAS Geology Dept. No. 58372. (*C*) *Syngnathus emeritus*, LACM 27445.

ly except that she incorrectly stated that scutella are absent.

Hipposyngnathus Danil'chenko

Hipposyngnathus DANIL'CHENKO, 1960:87 (type-species by original designation *H. convexus* Danil'chenko); JERZMANSKA 1968:436.

DIAGNOSIS.—Lateral protecting plates of brood pouch absent, however, a very pronounced median ventral trunk ridge probably indicates position of brood area. Dorsal, pectoral, and caudal fins present. Dorsal mainly on the tail. Ridges of body generally moderately developed and rugose, but without spines or serrations. Three described species from the Oligocene and Miocene.

DISTRIBUTION.—Oligocene of the Caucasus and Carpathian Mountains of southeastern Europe. Miocene of southern California.

Hipposyngnathus imporcitor n.sp.

(Figure 15*A*)

Syngnathus avus (in part, not of Jordan and Gilbert, 1919): DAVID 1943:70 (description).

Holotype: LACM 12055, an almost-complete specimen from the upper Modelo Formation of the northeast slope of Santa Monica Mountains, Los Angeles County, California (Locality LACM (CIT) 326).

REFERRED MATERIAL (all from California).—Upper Modelo Formation, NE slope Santa Monica Mountains, Los Angeles County, 24 identifiable specimens, 33 fragments, LACM loc. no. (CIT)326: LACM cat. nos. 10060–10061, 10063, 10114, 10134, 10143, 10145, 12054, 25341–25351; and LACM loc. no. 1267: LACM cat. nos. 13362–13373, 13451–13465, 13469–13473, 13475, 13477–13478, 25789–25791. Near Lompoc, LACM loc. no. 6589, 10 fragmentary specimens: LACM cat. nos. 12160–12169. Near Emery Park, Alhambra, Los Angeles County, LACM loc. nos. 1031, 1033, 14 specimens: LACM cat. nos. 1056–1058, 1349, 12459–12464, 25668. Dixie Canyon, Santa Barbara County, LACM loc. no. (CIT)329, 6 specimens: LACM cat. nos. 25357–25359, 25363–25365.

DIAGNOSIS.—A *Hipposyngnathus* from the upper Modelo Formation of southern California with about 22 dorsal rays; 20–22 trunk rings; 42–44 tail rings; snout 1.5–1.9 in head; orbit 7.8–12.0 in head; pouch rings equal to trunk rings; pectoral fin present but rays not countable; pouch ridge as long as adjacent trunk. Maximum size known 242 mm SL.

DESCRIPTION.—Body ridges moderately developed and rugose. Plates rhomboid-ovate with 10–13 ridgelets on either side of median ridge, large; each trunk plate about as wide as orbit. Opercular ridge smooth, about half as long as opercle. Snout without distinct ridge. Scutella small. Two infraorbitals. Vertebrae as in *Syngnathus*. Dorsal high, about 1.5 times higher than adjacent tail. Caudal normally developed.

DISCUSSION.—*H. imporcitor* is the most common syngnathid in the upper Modelo Formation. The extinct *Hipposyngnathus* was previously known from two European Oligocene species. *Hipposyngnathus imporcitor* can be easily distinguished from its congeners *H. neriticus* and *H. convexus* by the characters given in the diagnosis.

The genus *Hipposyngnathus* is unusual in having a very exaggerated ventral trunk ridge. Jerzmanska (1968) suggested that the males alone had this ridge and that it was the site of egg deposition. She also speculated that pouch flaps were present on either side of the ridge. However, the extant genus *Maroubra* also has an enlarged ventral trunk ridge, although not so well developed as in *Hipposyngnathus*, and its eggs are not protected by flaps. It seems improbable that *Hipposyngnathus* had brood-pouch flaps.

The Gastrophori are typically spiny with the exception of *Nerophis* and *Entelurus*. *Hipposyngnathus* is most like *Nerophis* in general body form.

PALEOECOLOGY.—Crane (1966) has discussed the paleoecology of *Chauliodus eximius*, a chauliodontid from the diatomite of the upper Modelo. Most of his specimens were from the same localities as those where *Hipposyngnathus* was collected. The upper Modelo is approximately 15 million years old (Crane 1966).

David (1943) discussed the paleoecology and climate of the upper Sisquoc Formation and the deposits at Lompoc. She concluded that the Lompoc deposits were younger and that the fishes found there were neritic and pelagic, and those of the upper Modelo more bathypelagic. Her conclusion that the fish fauna of the upper Modelo indicated a basin depth of 200–500 m is probably in error. Recent evidence (Crane 1966) supports the view that the basin was probably at least 1000 m in depth.

With the above evidence in mind, it seems most probable that *H. imporcitor* was a pelagic species, which may have accompanied floating algae, much as do the Recent species *Syngnathus pelagicus* and *S. californiensis*. This conclusion is supported by the evidence presented by Danil'chenko (1960) for the fishes of the Maikop basin. He showed that this basin was anoxic below a depth of 300 m, therefore *H. convexus* may be assumed to be a pelagic species.

ETYMOLOGY.—From the Latin *Imporcitor*—"a diety that presides over the drawing of furrows," in reference to the greatly expanded trunk ridge. To be treated as a noun in apposition and as of masculine gender.

Syngnathus Linnaeus

Syngnathus emeritus n.sp.

(Figure 15*C*)

Holotype: LACM 27445, an almost complete specimen from the Puente Formation near San Dimas, Los Angeles County, California (Locality LACM 7153).

REFERRED MATERIAL.—Puente Formation near San Dimas, Los Angeles County, California, LACM loc. nos. 5153, 7046, 14 specimens and fragments: LACM 26146–26148, 27431–27434, 27437–27440, 27446–27448.

DIAGNOSIS.—A *Syngnathus* with 43–47 dorsal rays; 10 caudal rays; pectoral rays not detectable; 14–15 trunk rings; 51 tail rings; snout 1.5–1.8 in head; orbit 5.8–8.7 in head; brood pouch not seen; largest specimen examined 181 mm SL.

DESCRIPTION.—Ridges of body smooth and generally not accentuated. Osteology basically the same as in extant species of *Syngnathus*. Plates small, width of trunk plate less than orbit diameter. Dorsal about as high as depth of adjacent body.

COMPARISONS.—*S. emeritus* is unusual in having 15 trunk rings combined with 51 tail rings. These characters and the number of dorsal rays distinguish it from *S. avus*.

The relationships of *S. emeritus* perhaps lie with the extant species *S. leptorhynchus* and *S. auliscus*. It is possible that *S. emeritus* was on the ancestral line leading to one or both of these species.

ETYMOLOGY.—From the Latin *emeritus*—honorably retired.

PALEOECOLOGY.—*S. emeritus* is found in the diatomaceous shale of the Puente Formation. Its habits probably were much like those of *S. avus*, i.e., living in relatively shallow water among marine vegetation.

Syngnathus avus (Jordan and Gilbert)

(Figure 15*B*)

Syngnathus avus Jordan and Gilbert, 1919:34 (Miocene chalk near Titus Avenue, Bairdstown, California, U.C. loc. no. 3525; type-specimen by original designation, SU XLIV, B of original description): Jordan 1921:259 (reconstruction); David 1943:70 (in part; description; synonymy).

Syngnathus californiensis avus: Herald 1941:69 (description; discussion).

Holotype: CAS Geology Dept. no. 58372 (SU no. XLIV, B of original description), all fossil fish types and other Jordan paleoichthyological material is now in the Geology Department, California Academy of Sciences.

Paratypes: CAS Geology Dept. no. 58373 (SU no. V, also marked 115, A of original description); CAS Geology Dept. no. 58374 (SU no. 115A, C of original description).

Referred Material.—Lower Modelo Formation, Santa Monica Mountains, Los Angeles County, California, LACM loc. no. 1681, 15 specimens: LACM cat. nos. 11598–11605, 26438–26444.

Diagnosis.—A *Syngnathus* with 36 dorsal rays; 10 caudal rays; 18 trunk rings; 43 tail rings; dorsal on 0.5 + 7.5 rings; pouch covering 22 rings; head 6.4–7.0 in SL; snout 1.7–1.8 in head; dorsal fin base 1.3 in head; maximum known size 225 mm SL.

Description.—Generally as given by Jordan and Gilbert (1919). Osteology of neurocranium same as that described for extant species of *Syngnathus* (Jungersen 1910). Opercles without median ridge.

Discussion.—The type material is now in such poor condition that the characters as given by Jordan and Gilbert (1919) cannot accurately be determined. However, specimen No. 58373 (paratype) does have a brood pouch with protecting plates developed; they are not missing as stated by Herald (1941).

Syngnathus avus is a rather common member of the fossil fauna of the argillaceous diatomites of the lower Modelo Formation. The original field notes indicate that one slab measuring 4 by 4 ft [1.2 × 1.2 m] contained 42 specimens.

It must be pointed out that Figure 2 on Plate XXIX of Jordan and Gilbert (1919) is not of the type of *S. avus*. In fact, Jordan and Gilbert mistakenly included a figure of a fossil pipefish from Austria rather than the correct figure of *S. avus*. This mistake was pointed out by Duncker (1923) and was subsequently corrected by Jordan (1926, 1927).

Distribution and Relationships

The eastern Pacific syngnathids are generally distributed, with some exceptions, in commonly recognized zoogeographic provinces. Most of the pipefishes are found in bays and sloughs where the water temperature may be higher than along the adjacent open coast. As a result their distribution often extends past the higher-latitude, colder-water boundary established for the open-coast fauna. This kind of distribution is shown by other bay-dwelling fishes such as the blennies and gobies (distributions in Miller and Lea 1972). For example, *Hypsoblennius gentilis* ranges from the Gulf of California to Monterey, *Ilypnus gilberti* ranges from the Gulf of California to Tomales Bay, *Clevelandia ios* ranges from the Gulf of California to British Columbia, and *Quietula y-cauda* ranges from the Gulf of California to Morro Bay. *Syngnathus leptorhynchus* ranges from the outer coast of Baja California to southern Alaska. Thus, these bay-dwelling fishes cross the Point Conception faunal boundary (Briggs 1974).

There are more species of *Syngnathus* in the Northern Hemisphere than in the Southern Hemisphere. The close similarity of Japanese *Syngnathus schlegeli* to generalized members of two distinct eastern Pacific lineages supports the hypothesis that the eastern Pacific *Syngnathus* are derivable from two separate invasions from the northwest. An alternative hypothesis is invasion of Japan from the eastern Pacific followed by a reinvasion of the eastern Pacific. However, the first hypothesis appears to be the most parsimonious. One lineage consists of *S. carinatus*, *S. macrobrachium*, and *S. folletti*. The other consists of *S. leptorhynchus*, *S. euchrous*, and *S. insulae*. The related *S. californiensis* and *S. exilis* occupy a somewhat isolated position in the genus and may be the products of another radiation.

The problem of defining these lineages and relating them to *S. schlegeli* is one of not being able to determine plesiomorphic and apomorphic character states at the species level within the genus *Syngnathus*. Thus, overall similarities, including meristic characters and strength of ridge development, become the most important criteria used.

The *carinatus-macrobrachium-folletti* lineage is characterized by a relatively long snout; large, well-developed fins; large orbit; and rather well-developed ridges. The presence of *carinatus* in the upper Gulf of California and *macrobrachium* and *folletti* in South America parallels the distribution given by Chen (1975) for the *exsul-spinorbis* and *capensis* complexes of the subgenus *Sebastomus*. Chen speculated that these lineages probably shared a common ancestor that was able to both invade the Gulf and cross the tropics using the same climatic event. He was, however, unable to rule out multiple crossings. The lack of any close relative of *S. carinatus* along the outer coast of Baja California or California is puzzling and quite different from the *Sebastomus* example given above. It is possible that the *carinatus-macrobrachium-folletti* lineage may have had a southern origin, although more evidence is needed in support of this hypothesis.

The *leptorhynchus-euchrous-insulae* lineage is characterized by the medium-length snout, which is round in cross section, and an almost straight snout ridge which does not rise much anterior to the orbit. The restriction of this group essentially to Baja California northward is interpreted to mean that, assuming a more northern origin, this lineage is much more recent than the preceding one.

It is apparent that *S. leptorhynchus* has given rise to the Guadalupe Island endemic *S. insulae*, probably as a result of waif dispersal via the California Current.

Syngnathus leptorhynchus and *S. euchrous* probably share a common ancestor. The isolation of a population of *S. euchrous* in Turtle Bay has produced the subspecies *S. e. ollotropis*. Turtle Bay is unusually warm and the *Macrocystis pyrifera* found there has a different growth form than that along the coast (Neushul 1971). A zone of intergradation between *S. e. euchrous* and *S. e. ollotropis* exists at Puerto Malarrimo.

Syngnathus exilis and *S. californiensis* are characterized by an elongate, compressed snout, and rounded ridges. It is possible that they are related to the *carinatus-macrobrachium-folletti* lineage, but their relationships cannot be determined at this time.

The relationships of the fossil *S. avus* and *S. emeritus* are difficult to determine. It seems highly probable that *S. avus* is related to the generalized *S. leptorhynchus* based mainly on meristic characters. The low trunk ring and high tail ring counts of *S. emeritus* are unlike those seen in living eastern Pacific *Syngnathus* spp.

Syngnathus auliscus is the only truly tropical member of the genus *Syngnathus* in the eastern Pacific. The characteristic spination of young *S. auliscus* can also be seen in young *S. fuscus* from the northwestern Atlantic. This spination has also been reported (D'Ancona 1933) for the Mediterannean *S. agassizi* and *S. phlegon*. Spination in young *Syngnathus* may be indicative of a distinct lineage within the genus. A systematic study of the juveniles of *Syngnathus* spp. is definitely called for.

Syngnathus auliscus is not uncommonly taken in southern California. It is apparent that this species is little affected by the tropical-temperate transition between about Sebastián Vizcaíno Bay and Magdalena Bay. This distribution pattern is shown by other fishes such as *Paralabrax maculatofasciatus* (distribution in Miller and Lea 1972). However, in San Diego Bay the warm-water effluent produced by the San Diego Gas and Electric power plant provides an ideal environment for tropical species. As a result there is a large population of *S. auliscus* in San Diego Bay, and the typical California bay species *S. leptorhynchus* is now less abundant.

The genus *Bryx* is a circumtropical genus with only *B. arctus* and *B. heraldi* having temperate populations. There are eight species in the New World; one, *B. balli*, is in Hawaii, *B. banneri* is in the Indo-West Pacific, and *B. darrosanus* is in the Indian Ocean. The two subgenera, *Bryx* and *Simocampus*, were present before the closure of the Panamanian seaway in the late Pliocene to early Pleistocene (Woodring 1966), since the eastern Pacific and western Atlantic now have members of both subgenera.

The subgenus *Bryx* is composed of four species, two in the Atlantic and two in the Pacific Ocean. This subgenus is presumably derived from the subgenus *Simocampus* and is distinguished from it by the absence of the anal fin. The two species in each ocean are more closely related to each other than either is to the species in the other ocean. In fact the radiations in the two oceans have paralleled each other. The primary difference between the two species is the relative length of the snout.

Without a knowledge of the plesiomorphic condition with regard to meristic characters, it is impossible to speculate on the relationships within the subgenus *Simocampus*. However, the Juan Fernández endemic *B. heraldi* was probably derived from *B. coccineus* or their immediate common ancestor. This is unusual since the ichthyofauna on the Chilean islands of Juan Fernández and San Félix has a strong Indo-Pacific component (McCosker 1970, 1971). The eastern Pacific *B. arctus* and *B. coccineus* are more closely related to each other than either is to members of the genus in other oceans.

Doryrhamphus melanopleura is an Indo-Pacific species that has apparently invaded the eastern Pacific by crossing the East Pacific Barrier, since there are no members of this genus in the Atlantic, even though suitable habitat would seem to be available. The eastern Pacific populations of *D. melanopleura* differ in coloration from their Indo-West Pacific conspecifics. The Islas Revillagigedo endemic *D. paulus* has the same color pattern as the eastern Pacific *D. melanopleura* and was probably derived from mainland populations of *D. melanopleura*.

The genus *Leptonotus* is a southern cold-temperate group with species in South Australia (Munro 1958), New Zealand, and southern South America. This genus is represented in South America by *L. blainvilleanus*. The mechanism by which cold-temperate organisms have achieved a distribution spanning the South Pacific Ocean is currently under debate. Rosen (1974) has argued that the distribution of at least the freshwater galaxiids covers most of the components of the original Gondwanaland mass. Thus, the distribution of southern cold-temperate organisms reflects the break-up of Gondwanaland. However, the possibility of chance dispersal probably utilizing the eastward-flowing South Pacific current seems to be more likely for most marine fishes. This has been documented by McCosker (1970, 1971) for *Parapercis* and *Muraenichthys*. McCosker pointed out that most of the groups showing this particular distribution pattern are derived from Indo-West Pacific groups dispersing southward to southern Australia and New Zealand, and the subsequent movement eastward of cold-adapted forms across the cold-temperate South Pacific Ocean to Chile. Eschmeyer and Poss (1976) have shown that with some cooling during the Pleistocene, a number of near-surface sea mounts, reefs, and islands would have been available to eastward-moving temperate biota in the southern Pacific Ocean. Although they were dealing with the scorpionfish genus *Maxillicosta*, the effects of Pleistocene or earlier cooling would also facilitate dispersal of *Leptonotus*. The ability of marine fishes to cross oceanic barriers has been well documented (Rosenblatt et al. 1972). Pipefishes (e.g., *S. pelagicus*) are known to be borne great distances by the currents. It is therefore likely that the marine *L. blainvilleanus* was derived from an ancestor from the South Australia–New Zealand region by chance dispersal of waifs to South America.

The relationships of *Hippocampus* must await a revisionary study of the genus *Hippocampus*. Our knowledge of the genus *Hippocampus* is so poor that it is now impossible to determine the exact relationship of *H. ingens* to other members of the genus. Since the genus is circumtropical, it is at least pre-Tethyan in origin.

Hipposyngnathus has become extinct since the Tertiary. Because of our almost complete ignorance of the relationships between genera of living syngnathids, it is impossible to relate *Hipposyngnathus* to living genera. The reason or reasons for the extinction of this genus remain unknown.

Branchial Skeleton

Previous investigators (Duncker 1910, 1912; and Herald 1959) have used the position and development of the male brood pouch as the diagnostic character when defining genera and subfamilies. The method of brood pouch closure was used by Herald (1959) in constructing a phylogeny of the Syngnathidae.

The few osteological studies which have included the Syngnathidae have generally been based on only one or a few of the genera (Jungersen 1910; Banister 1967). These studies were therefore not adequately comparative and provided little information on intrafamilial relationships.

In order better to characterize the genera and subfamilies within the Syngnathidae, I have begun a study of the osteology of the syngnathid genera. This study is also designed to be a test of the hypotheses of relationships presented by previous authors who studied the brood pouch. Although the present investigation is still preliminary, data can be presented at this time.

Because the syngnathids are such highly specialized fishes, many aspects of their osteology (e.g., caudal skeleton) are so reduced that they can provide little phylogenetic information. However, the branchial skeleton does seem to provide useful information. All the genera ex-

TABLE 9. SYNGNATHID BRANCHIAL FORMULAE.

Genus	B1	B2	B3	H1	H2	E1	E2	E3	I2	I3	Remarks
GASTROPHORI:											
Heraldia (1)*	+	+	+	+	+	+	+	+	+	+	
Maroubra (1)	+	+	−	+	+	+	+	+	+	+	
Choeroichthys (1)	+	+	−	+	+	+	+	+	+	+	
Dentirostrum (1)	+	+	−	+	+	+	+	+	+	+	
Doryrhamphus (1)	+	+	−	+	+	+	+	+	+	+	
Dunckerocampus (1)	+	+	−	+	+	+	+	+	+	+	
Syngnathoides (1)	+	+	−	+	−	−	−	−	+	+	1
Nerophis (1)**	+	+	−	+	−	−	−	−	+	−	
UROPHORI:											
Leptonotus (1)	+	+	−	+	+	+	+	+	+	+	
Parasyngnathus (1)	+	+	−	+	+	+	+	+	+	+	2
Ichthyocampus (1)	+	+	−	+	+	+	+	+	+	+	
Micrognathus (1)	+	+	−	+	+	+	+	+	+	+	3
Syngnathus (7)†	+	+	−	−/r	+	+	+	+	+	+	
"*Corythoichthys*" (Atl.) (1)	+	+	−	+	r	+	+	+	+	+	
Bryx (*Bryx*) (3)	+	+	−	+	r	+/r	r	+	+	+	
Bryx (*Simocampus*) (2)	+	+	−	+	r	+/r	r	+	+	+	
Pseudophallus (2)	+	+	−	−	+	+	+	−	+	+	
Hippocampus (2)	−	−	−	+	+	+	+	+	+	+	
Phyllopteryx (1)	−	−	−	+	−	−	−	?	+	+	4
Corythoichthys (Pac.) (2)	+	−	−	−	+	−	−	−	−	−	
Penetopteryx (1)	+	+	−	+	+	+	+	+	+	+	

\+ = present.
− = absent.
r = reduced.
* Number in parenthesis represents number of species examined.
** Data from Jungersen (1910).
† Only *Syngnathus acus* has reduced H1.
1 I2&3 with tooth plates.
2 with additional 1 element.
3 I2&3 with tooth plates.
4 I2&3 with tooth plates.

amined so far (Table 9) have a full complement of ceratobranchials (i.e., five pairs). The remaining elements in the branchial skeleton are variously lost or reduced within the family and possibly along distinct lineages within the family. The Urophori in particular show reduction and loss of every element except the ceratobranchials. The structure of the branchial skeleton is constant within a genus. Although the information provided by the branchial skeleton is based on characters undergoing reduction and not on uniquely derived characters, it is reasonable to use these characters when defining relationships. It seems quite probable that an element which is lost from such a highly evolved structure would not be regained.

The presence of well-developed first hypobranchials and reduced second hypobranchials and epibranchials clearly distinguish the genus *Bryx* from *Syngnathus* (Fig. 16). *Bryx* was included by Herald (1959) as a subgenus of *Syngnathus*.

The loss of all elements except the first basibranchial and second hypobranchials in the Pacific species usually referred to the genus *Corythoichthys* is clear evidence that the Atlantic and Pacific species should be placed in separate genera (Fig. 17). In fact, Dawson (1977) provisionally referred Atlantic species of *Corythoichthys* to the catchall genus *Syngnathus* and more recently placed them in a new genus, *Cosmocampus* (Dawson 1979). Herald's hypothesis that *Corythoichthys* is ancestral to, or on the lineage leading to, *Syngnathus* is clearly erroneous. However, Atlantic species of *Cosmocampus* could very well be on the lineage leading to *Bryx*.

Herald's hypothesis that *Leptonotus* and *Mi-*

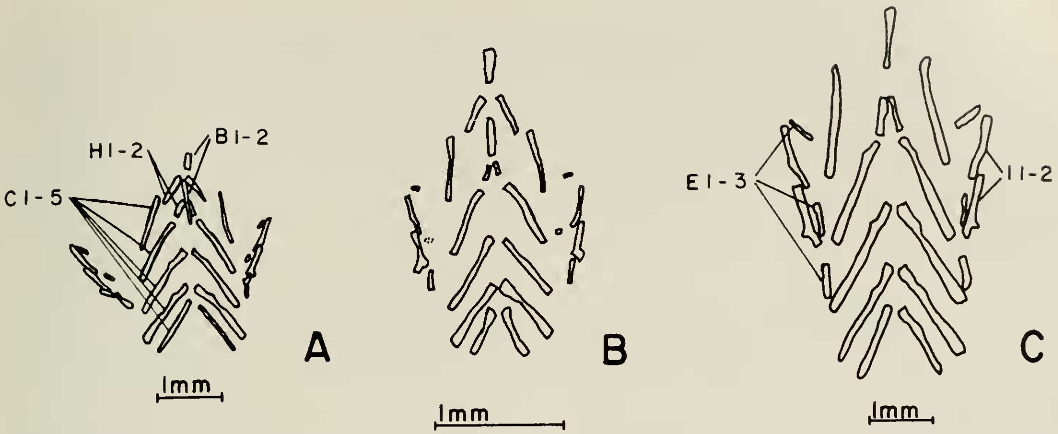

FIGURE 16. Dorsal view of the branchial skeleton of several syngnathids with the epibranchials and infrapharyngobranchials shown from their ventral aspect. (*A*) *Parasyngnathus elucens*, CAS 13696. (*B*) *Bryx arctus*, SIO H52-218. (*C*) *Syngnathus californiensis*, SIO H47-180. Abbreviations: B—basibranchial; H—hypobranchial; C—ceratobranchial; E—epibranchial; I—infrapharynogobranchial.

crognathus are derivable from *Parasyngnathus* can neither be supported nor refuted on the basis of their branchial skeletons. *Parasyngnathus* has a primitive branchial skeleton (Fig. 16). The retention of the upper pharyngeal tooth plates in *Micrognathus* is the only major difference between it and *Parasyngnathus*.

One interesting point is the extreme reduction of the branchial skeleton in the gastrophorine genus *Syngnathoides* and in the urophorine genera *Phyllopteryx* and *Hippocampus* (Fig. 17). These three genera are presently placed in separate subfamilies because of differences in the position and development of the brood pouch. However, in addition to the reduction of branchial elements, all three genera have the head at an angle to the main body axis and a prehensile tail without a caudal fin. This evidence may indicate that the three genera are much more closely related than has previously been recognized.

The amount of variation in the branchial skeleton is much greater in the Urophori than in the Gastrophori. The Gastrophorine genus *Heraldia* is the only syngnathid genus with three basibranchials, and it might well be the most primitive of the syngnathid genera.

The genus *Nerophis* is usually considered to be the most primitive genus in the family. However, the species referred to this genus have the most specialized branchial skeleton, in terms of reduction, in the Gastrophori (Table 9).

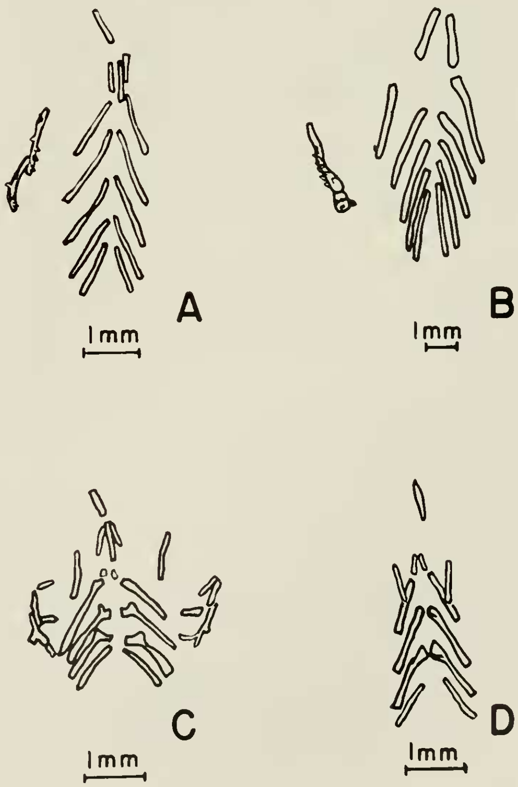

FIGURE 17. Branchial skeletons of four syngnathids. (*A*) *Syngnathoides biaculeatus*, SIO 60-693. (*B*) *Phyllopteryx foliatus*, SIO 73-361. (*C*) *Cosmocampus brachycephalus*, CAS 24025. (*D*) *Corythoichthys intestinalis*, SIO 73-206.

The evidence as is cited above indicates that the structure and development of the branchial skeleton in the Syngnathidae is of great utility in determining relationships. The fact that relationships as determined by the branchial skeleton transcend recognized subfamilial boundaries is a strong indication that the within-family relationships of this group are far from being understood.

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Literature Cited

Anonymous. 1921. Dredging and hydrographic records of the U.S. Fisheries Steamer "Albatross" 1911–1920. Appendix 3, Rep. U.S. Comm. Fish. 1920, Doc. 897, 190 p.

Abbott, J. F. 1899. The marine fishes of Peru. Proc. Acad. Nat. Sci. Phila. 1899:324–364.

Alverson, F. G. 1963. The food of yellowfin and skipjack tunas in the eastern tropical Pacific Ocean. Inter-Amer. Trop. Tuna Comm. Bull. 7:293–396.

Atz, J. W. 1937. Neptune's knight: the seahorse. Bull. N.Y. Zool. Soc. 40(2):57–65.

Ayres, W. O. 1854. Description of *Syngnathus griseo-lineatus*. Pacific 3(51):202.

Banister, K. E. 1967. The anatomy and classification of the order Gasterosteiformes (Pisces). Ph.D. Dissertation. University of Newcastle upon Tyne, England. 211 p.

Barnhart, P. S. 1936. Marine fishes of southern California. Univ. Calif. Press, Berkeley. 209 p.

Berry, F. H., and H. C. Perkins. 1965. Survey of pelagic fishes of the California Current area. U.S. Fish Wildl. Serv. Fish. Bull. 65(3):625–682.

Bleeker, P. 1858. Vijfde bijdrage tot de kennis der ichthyologische fauna van de Kokos-eilanden. Nat. Tijdsch. Neder. Indie. 15:457–468.

Bonaparte, C. L. J. L. 1838. Synopsis vertebratorum systematis. Nuov. Ann. Sci. Nat. 2:105–133.

Breder, C. M., Jr. 1928. Scientific results of the second oceanographic expedition of the "Pawnee" 1926. Nematognathi, Apodes, Isospondyli, Synentognathi, and Thoracostraci from Panama to Lower California with a generic analysis of the Exocoetidae. Bull. Bing. Oceanogr. Exped. 2(2):1–25.

Briggs, J. C. 1974. Marine Zoogeography. McGraw-Hill, New York. 475 p.

Brown, J. 1972. A comparative life history study of four species of pipefishes (family Syngnathidae) in Florida. Ph.D. Dissertation. University of Florida, Gainesville. 163 p.

Brothers, E. B. 1975. The comparative ecology and behavior of three sympatric California gobies. Ph.D. Dissertation. University of California, San Diego. 370 p.

Castro-Aguirre, J. L., J. Arvizu-Martínez, and J. Páez-Barrera. 1970. Contribución al conocimiento de los peces del Golfo de California. Rev. Soc. Méx. Hist. Nat. 31:107–181.

Chen, L. 1975. The rockfishes, genus *Sebastes* (Scorpaenidae), of the Gulf of California, including three new species, with a discussion of their origin. Proc. Calif. Acad. Sci., Ser. 4, 40(6):109–141.

Chirichigno-F., N. 1963. Estudios de la fauna ictíologia de los esteros y parte baja de los rios de departmento de Tumbes (Perú). Servicio de Pesquería Perú, Serie de Divulgación Cientifica, No. 22. 87 p.

———. 1974. Clave para identificar los peces marinos del Perú. Inf. Inst. Mar Perú-Callao, No. 44:1–387.

Clemens, H. B. and J. C. Nowell. 1963. Fishes collected in the eastern Pacific during tuna cruises, 1952 through 1959. Calif. Fish Game 49(4):240–264.

Crane, J. M., Jr. 1966. Late Tertiary radiation of viperfishes (Chauliodontidae) based on a comparison of recent and Miocene species. Los Angeles Cty. Mus. Contrib. Sci., no. 115:1–29.

D'Ancona, U. 1933. Family Syngnathidae. *In* Fauna e Flora del Golfo di Napoli, 38. Monografia: Uova, larve, e stadi giovanili di teleostei (Monografia eleborata con l'uso del materiale raccolto e seriato da Salvatore Lo Bianco). Stn. Zool. Napoli, pt. 2:284–299. [Translation of the Israel Program for Scientific Translation 1969]

Danil'chenko, P. G. 1960. Kostistye ryby maikopskich otlozenii kavkaza. Tr. Paleontol. Inst. Akad. Nauk SSSR 78:3–207.

David, L. R. 1943. Miocene fishes of southern California. Geol. Soc. Am. Spec. Pap. no. 43:1–143.

Dawson, C. E. 1977. Review of the pipefish genus *Corythoichthys* with description of three new species. Copeia 1977(2):295–338.

———. 1979. Notes on western Atlantic pipefishes with description on *Syngnathus caribbaeus* n.sp. and *Cosmocampus* n.gen. Proc. Biol. Soc. Wash. 92(4):671–676.

———, and R. A. Fritzsche. 1975. Odontoid processes in pipefish jaws. Nature 257:390.

———, and J. E. Randall. 1975. Notes on Indo-Pacific pipefishes (Pisces: Syngnathidae) with description of two new species. Proc. Biol. Soc. Wash. 88(25):263–280.

Dawson, E. Y. 1944. The marine algae of the Gulf of California. Allan Hancock Pac. Exped. 3(10):189–464.

DeBuen, F. 1963. Peces Chilenos Beloniformes, Syngnathiformes y Gobiidae. Bol. Soc. Biol. Concepción 35–36(1960–61):82–101.

Delfin, F. T. 1901. Catálogo de los peces de Chile. Rev. Chilena Hist. Nat. 3(1899) and 4(1900). 133 p.

Dixon, W. J., and F. J. Massey, Jr. 1957. Introduction to statistical analysis. 2nd ed. McGraw-Hill, New York. 488 p.

Duméril, A. H. A. 1870. Histoire naturelle des poissons ou ichthyologie générale. Vol. 2. Paris. 624 p.

Duncker, G. 1908. Syngnathiden-Studien. I. Variation und Modifikation bei *Siphonostoma typhle* L. Mitt. Naturh. Mus. (Jahrb. Wiss. Anst.) Hamburg 25:1–115.

———. 1912. Die Gattungen der Syngnathidae. Ibid. 29(2):219–240.

———. 1915. Revision der Syngnathidae. Erster teil. Ibid. 32:9–120.

———. 1923. Warnung. Zool. Anz. 56:238–239.

Eigenmann, C. H., and R. S. Eigenmann. 1892. A catalogue of the fishes of the Pacific coast of America, north of Cerros Island. Ann. N.Y. Acad. Sci. 6:349–358.

Eschmeyer, W. N., and S. G. Poss. 1976. Review of the scorpionfish genus *Maxillicosta* (Pisces:Scorpaenidae), with a description of three new species from the Australian-New Zealand region. Bull. Mar. Sci. 26(4):433–449.

Evermann, B. W., and O. P. Jenkins. 1891. Report upon a collection of fishes made at Guaymas, Sonora, Mexico, with descriptions of new species. Proc. U.S. Natl. Mus. 1891:121–165.

———, and H. B. Latimer. 1910. On a collection of fishes from the Olympic Peninsula, together with notes on other west coast species. Proc. Biol. Soc. Wash. 23:131–139.

———, and L. Radcliffe. 1917. The fishes of the west coast of Peru and the Titicaca Basin. Bull. U.S. Natl. Mus. 95:1–166.

Eydoux, F., and P. Gervais. 1837. Voyage de "La Favorite." Poissons. *Echeneis sexdecim-lamellata* et *Syngnathus blainvilleanus*. Mag. Zool. 7:1–4.

Feder, H. M., C. H. Turner, and C. Limbaugh. 1974. Observations on fishes associated with kelp beds in southern California. Calif. Dep. Fish Game Fish. Bull. no. 160:1–144.

Fischer, W. 1963. Die Fische des brackwassergebiets Lenga bei Concepcion (Chile). Int. Rev. Gesamten Hydrobiol. 48:419–511.

Fowler, H. W. 1921. Notes on hemibranchiate and lophobranchiate fishes. Proc. Acad. Nat. Sci. Phila. 73:437–448.

———. 1944a. Fishes obtained in the New Hebrides by Dr. Edward L. Jackson. Proc. Acad. Nat. Sci. Phila. 96:155–199.

———. 1944b. Results of the Fifth George Vanderbilt Expedition (1941). The fishes. Monogr. Acad. Nat. Sci. Phila. no. 6:57–583.

Gilbert, C. H. 1891. Scientific results of explorations by the U.S. Fish Commission Steamer Albatross. No. XIX.—A supplementary list of fishes collected at the Galapagos Islands and Panama, with descriptions of one new genus and three new species. Proc. U.S. Natl. Mus. 1890, 13:449–455.

———. 1892. Scientific results of explorations by the U.S. Fish Commission Steamer Albatross. No. XXII.—Descriptions of thirty-four new species of fishes collected in 1888 and 1889, principally among the Santa Barbara Islands and in the Gulf of California. Proc. U.S. Natl. Mus. 14:539–566.

———, and C. C. Starks. 1904. The fishes of Panama Bay. Mem. Calif. Acad. Sci. 4:1–304.

Gill, T. N. 1863. Synopsis of the species of lophobranchiate fishes of western North America. Proc. Acad. Nat. Sci. Phila. 1862:282–284.

———. 1905. The life-history of the sea-horses (Hippocampids). Proc. U.S. Natl. Mus. 28:805–814.

Ginsburg, I. 1933. Descriptions of five new species of seahorses. J. Wash. Acad. Sci. 23(12):560–563.

———. 1937. Review of the seahorses (*Hippocampus*) found on the coasts of the American continents and of Europe. Proc. U.S. Natl. Mus. 83:497–594.

Girard, C. F. 1854. Observations upon a collection of fishes made on the Pacific Coast of the United States by Lieut. W. P. Trowbridge, U.S.A., for the museum of the Smithsonian Institution. Proc. Acad. Nat. Sci. Phila. (for 1854), 7(4):142–156.

———. 1859. Fishes. *In* General Report upon the Zoology of the several Pacific railroad routes, 1857. U.S. Senate Miscell. Doc. no. 78, 1859, 33 Congr., 2 Sess. 400 p.

Guichenot, A. 1848. Fauna Chilena. Peces. *In* Gay, C., Historia fisica y politica de Chile . . . , Paris, ("en casa del Autor") Zoología 2:137–372.

Günther, A. 1870. Catalog of the fishes in the British Museum. Vol. 8. Taylor and Francis, London. 549 p.

Herald, E. S. 1940. A key to the pipefishes of the Pacific American coasts with descriptions of new genera and species. Allan Hancock Pac. Exped. 9(3):51–64.

———. 1941. A systematic analysis of variation in the western American pipefish, *Syngnathus californiensis*. Stanford Ichthyol. Bull. 2(3):49–73.

———. 1943. Studies on the classification and relationships of the American pipefishes. Ph.D. Dissertation. Stanford University. 339 p.

———. 1953. Family Syngnathidae:Pipefishes. Pp. 231–278 *in* Leonard P. Schultz et al. Fishes of the Marshall and Marianas Islands. Bull. U.S. Natl. Mus. 202, 1.

———. 1959. From pipefish to seahorse—a study of phylogenetic relationships. Proc. Calif. Acad. Sci. ser. 4, 29(13):465–473.

———. 1965. Studies on the Atlantic American pipefishes with descriptions of new species. Proc. Calif. Acad. Sci. ser. 4, 32(12):363–375.

Hildebrand, S. F. 1946. A descriptive catalog of the shore fishes of Peru. Bull. U.S. Natl. Mus. 189:1–530.

HOESE, D. E. 1971. A revision of the eastern Pacific species of the gobiid fish genus *Gobiosoma*, with a discussion of relationships of the genus. Ph.D. Dissertation. University of California, San Diego. 213 p.

HUBBS, C. L. 1916. Notes on the marine fishes of California. Univ. Calif. Publ. Zool. 16:153–169.

———. 1912. Notes on the pipe-fishes of California. Occas. Pap. Mus. Zool. Univ. Mich. no. 100:1–4.

———, AND K. F. LAGLER. 1958. Fishes of the Great Lakes region. Bull. Cranbrook Inst. Sci. 26:1–213.

———, AND S. D. HINTON. 1963. The giant sea horse returns. Pac. Discov. 16(5):12–15.

JENKINS, O. P., AND B. W. EVERMANN. 1888. Descriptions of eighteen new species of fishes from the Gulf of California. Proc. U.S. Natl. Mus. 1:137–158.

JENYNS, L. 1842. Fish. *In* Darwin, C., ed., The zoology of H.M.S. "Beagle," during the years 1832–1836. Part 4. 172 p.

JERZMANSKA, A. 1968. Ichtyofaune des couches à ménilite (flysch des Karpathes). Acta Palaeontol. Pol. 13(3):379–488.

JORDAN, D. S. 1895. The fishes of Sinaloa. Proc. Calif. Acad. Sci. ser. 2, 5:377–514.

———. 1921. The Miocene shore-fishes of California. Sci. Mon. 13(5):459–563.

———. 1926. Ein unglückliches Versehen. Zool. Anz. 6:221–224.

———. 1927. A confusing error. Copeia 1927(161):190–191.

———, AND B. W. EVERMANN. 1896. The fishes of North and Middle America. Part 1. Bull. U.S. Natl. Mus. 47:1–954.

———, AND ———. 1927. New genera and species of North American fishes. Proc. Calif. Acad. Sci. ser. 4, 16(5):501–507.

———, ———, AND H. W. CLARK. 1930. Checklist of the fishes and fish-like vertebrates of North and Middle America north of the northern boundary of Venezuela. Rep. U.S. Comm. Fish. (1928) pt. 2:1–670.

———, AND C. H. GILBERT. 1880. Notes on a collection of fishes from San Diego, California. Proc. U.S. Natl. Mus. 3:23–34.

———, AND ———. 1881. List of the fishes of the Pacific Coast of the United States, with a table showing the distribution of the species. Proc. U.S. Natl. Mus. 3:452–458.

———, AND ———. 1882. Notes on the fishes of the Pacific Coast of the United States. Proc. U.S. Natl. Mus. 4:29–70.

———, AND ———. 1883. Synopsis of the fishes of North America. Bull. U.S. Natl. Mus. 16:1–1018.

———, AND J. Z. GILBERT. 1919. Fossil fishes of southern California. II. Fossil fishes of the Miocene (Monterey) formations of southern California. Stanford Univ. Publ. (Univ. Ser.):13–60.

———, AND P. L. JOUY. 1882. Checklist of duplicates of fishes from the Pacific Coast of North America, distributed by the Smithsonian Institution in behalf of the United States National Museum. Proc. U.S. Natl. Mus. 4:1–18.

———, AND E. S. STARKS. 1896. Description of a new species of pipefish (*Siphostoma sinaloae*) from Mazatlan. Proc. Calif. Acad. Sci. ser. 2, 6:268.

JUNGERSEN, H. F. E. 1910. Structure of Aulostomidae, Syngnathidae, and Solenostomidae. K. Danske Vidensk. Skrift. Naturv., ser. 7, 8(5):268–384.

KAUP, J. J. 1853. Übersicht der Lophobranchier. Arch. Naturges. 19(1):226–234.

———. 1856. Catalogue of the lophobranchiate fishes in the collection of the British Museum. London. 76 p.

KERMODE, F. 1929. Report of the Provincial Museum of Natural History for the year 1928. [British Columbia] F1–F27.

———. 1930. Report of the Provincial Museum of Natural History for the year 1929. [British Columbia] F1–F26.

KOEPCKE, H. W. 1962. Lista de los peces marinas conocidos del Perú con datos de su distribución geográfica. Pt. 3. Biota 4(33):193–204.

LAIRD, A. K., A. D. BARON, AND S. A. TYLER. 1968. Growth and time: An interpretation of allometry. Growth 32:347–354.

LINNAEUS, C. 1758. Systema naturae. Regnum animale. 10th ed. Guiliemi Engelman, Lipsae. 824 p.

LOBELL, M. J. 1942. Some observations on the Peruvian coastal current. Trans. Am. Geophys. Union, pt. II:332–336.

MANN, F. G. 1954. La vida de los peces en aguas chilenas. Ministerio de Agricultura, Univ. of Chile, Santiago. 342 p.

MCCOSKER, J. E. 1970. A review of the eel genera *Leptenchelys* and *Muraenichthys*, with the description of a new genus, *Schismorhynchus*, and a new species, *Muraenichthys chilensis*. Pac. Sci. 24(4):506–516.

———. 1971. A new species of *Parapercis* (Pisces:Mugiloididae) from the Juan Fernandez Islands. Copeia 1971(4):682–686.

———, AND C. E. DAWSON. 1975. Biotic passage through the Panama Canal, with particular reference to fishes. Mar. Biol. 30:343–351.

MEEK, S., AND S. F. HILDEBRAND. 1923. The marine fishes of Panama, pt. 1. Field Mus. Nat. Hist. Publ. 215, zool. ser. 15:1–330.

MILLER, D. J. AND R. N. LEA. 1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game Fish Bull. no. 157. 235 p.

MORROW, J. E. 1957. Shore and pelagic fishes from Peru, with new records and the description of a new species of *Sphoeroides*. Bull. Bing. Oceanog. Coll. 26(2):5–55.

MUNRO, I. S. R. 1958. Syngnathiformes. Pp. 81–96 *in* Handbook of Australian fishes. Fish. Newsl. 17(2–5).

NEUSHUL, M. 1971. The species of *Macrocystis* with particular reference to those of North and South America. Pp. 211–222 *in* North, W. J., ed. The biology of giant kelp beds (*Macrocystis*) in California. Beihefte zur Nova Hedwigia 32.

NICHOLS, J. Y., AND R. C. MURPHY. 1922. On a collection of marine fishes from Peru. Bull. Am. Mus. Natl. Hist. 46:501–516.

———, AND ———. 1944. A collection of fishes from the Panama Bight, Pacific Ocean. Bull. Am. Mus. Nat. Hist. 83(4):217–260.

NORMAN, J. R. 1937. Coast fishes. Part II. The Patagonian region (including the Straits of Magellan and the Falkland Islands). Discovery Rep. 16:1–150.

OSBURN, R. C., AND J. T. NICHOLS. 1916. Shore fishes collected by the "Albatross" expedition in Lower California with descriptions of new species. Bull. Am. Mus. Nat. Hist. 35(16):139–181.

PHILIPPI, R. A. 1896. Peces nuevos de Chile. Anal. Univ. Chile 93:375–390.

RAFINESQUE, C. S. 1810. Caratteri de alcuni nuovi generi e nuove specie di animali e plante della Sicilia, con varie osservazioni sopra i medisimi. Palermo. 105 p.

RAUTHER, M. 1925. Die syngnathiden des Golfes von Neapel. Publ. Stn. Zool. Napoli 36:1–365.

Regan, C. T. 1908. Pisces. Biologia Centrali-Americana, 1906–1908. 203 p.

Ricker, K. E. 1959. Fishes collected from the Revillagigedo Islands during the 1954–1958 cruises of the "Marijena." Univ. Brit. Col. Inst. Fish. Mus. Contrib. no. 4:1–10.

Rosen, D. E. 1974. Phylogeny and zoogeography of salmoniform fishes and relationships of *Lepidogalaxias salamandroides*. Bull. Am. Mus. Nat. Hist. 153(2):267–325.

Rosenblatt, R. H. 1963. Some aspects of speciation in marine shore fishes. Pp. 171–180 *in* Speciation in the sea. Systematics Assoc. Publ. no. 5.

———, J. E. McCosker, and I. Rubinoff. 1972. Indo-west Pacific fishes from the Gulf of Chiriqui, Panama. Los Angeles Cty. Mus. Contrib. Sci. no. 234:1–18.

Schultz, L. P. 1957. The frogfishes of the family Antennariidae. Proc. U.S. Natl. Mus. 107:47–105.

Siccardi, E. M. 1954. Consideraciones sobre el modo de reproducción de "*Leptonotus blaenvillianus*" Eydoux and Gervais, 1837 (Pisces: Syngnath.). Comun. Inst. Nac. Invest. Cien. Nat. Cien. Zool. 2(14):211–242.

Snyder, J. O. 1911. Descriptions of new genera and species from Japan and the Riu Kiu Islands. Proc. U.S. Natl. Mus. 40:525–549.

Starks, E. C. 1911. Results of an ichthyological survey about the San Juan Islands, Washington. Ann. Carnegie Mus. 7:162–213.

———, and E. L. Morris. 1907. The marine fishes of southern California. Univ. Calif. Publ. Zool. 3:159–252.

Steindachner, F. 1898. Die Fische der Sammlung Plate. Fauna Chilensis. Zool. Jahrb. (Suppl.) 4:281–337.

Storer, D. H. 1848. Description of a new species of *Syngnathus*, brought from the western coast of California by Capt. Phelps. Proc. Boston Soc. Nat. Hist. 1845, 2(10):73.

Swain, J. 1882. A review of the Syngnathinae of the United States, with a description of one new species. Proc. U.S. Natl. Mus. 5:307–315.

———, and S. E. Meek. 1884. Notes on the pipefishes of Key West, Florida, with description of *Siphostoma McKayi*, a new species. Proc. U.S. Natl. Mus. 7:237–239.

Taylor, W. R. 1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus. 122:1–17.

Thompson, W. F. 1916. Fishes collected by the United States Bureau of Fisheries Steamer "Albatross" during 1888, between, Montevideo, Uruguay, and Tome, Chile, on the voyage through the Straits of Magellan. Proc. U.S. Natl. Mus. 50:401–476.

Ulrey, A. B. 1929. A check-list of fishes of southern California and Lower California. J. Pan-Pac. Res. Inst. 4(4):2–11.

———. 1932. Lista de los peces de las costas de la Baja California. Ann. Inst. Biol. 3(1):75–80.

———, and P. O. Greeley. 1928. A list of the marine fishes (Teleostei) of southern California with their distribution. Bull. South. Calif. Acad. Sci. 27(1):1–53.

Vaillant, L. L. 1883. Remarques sur les affinités naturelles des familles composant le sous-ordre des poissons malacoptérygiens abdominaux. Ann. Sci. Nat. (Zool.), sér. 6, 15(7):1–13.

———. 1888. Mission scientifique du Cap Horn, 1882–1883. VI. Zool., Poissons. Paris. 35 p.

———. 1894. Sur une collection de poissons recueillie en Basse-Californie et dans le Golfe par M. Léon Diguet. Bull. Soc. Philom. Paris, sér. 3, 6:69–75.

Waite, E. R. 1909. Subantarctic islands of New Zealand. Art. XXV. Vertebrata of the subantarctic islands of New Zealand. Pisces:585–598.

Weber, M. and L. F. de Beaufort. 1922. The fishes of the Indo-Australian Archipelago. IV. Leiden. 410 p.

Whitley, G. P. 1931. New names for Australian fishes. Aust. Zool. 6(4):310–334.

———. 1940. Illustrations of some Australian fishes. Aust. Zool. 9(4):397–428.

———. 1955. Sidelights on New Zealand ichthyology. Aust. Zool. 12(2):110–119.

Woodring, W. P. 1966. The Panama land bridge as a sea barrier. Am. Phil. Soc. 110(6):425–453.

Zweifel, J. R. and R. Lasker. 1976. Prehatch and posthatch growth of fishes—A general model. Fish. Bull., U.S. 74(3):609–621.

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